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Afterripening of Bromus Tectorum L. Seeds: Changes in Dormancy, Germination Rate, and Optimum Incubation Temperature

FINAL REPORT FOR RESEARCH AGREEMENT
#INT-92717-RJVA
Brigham Young University
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AFTERRIPENING OF BROMUS TECTORUM L. SEEDS: CHANGES IN DORMANCY, GERMINATION RATE, AND OPTIMUM INCUBATION TEMPERATURE[4]

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4This research was supported in part by funds provided by the Intermountain Research Station, Forest Service, U.S. Department of Agriculture.

Summary

Afterripening (i.e., changes in dormancy status and germination speed over a range of storage and subsequent incubation temperatures) was evaluated for seeds of Bromus tectorum. Seed collections from three contrasting habitats were stored from 10 to 40°C. At monthly intervals, subsamples were incubated at 5/15, 10/20, 15/25, and 20/30°C. For recently harvested seeds, initial 28-day germination ranged from 1 to 75%. Seeds were generally most dormant and slowest at high incubation temperatures; mean germination times were between 10 and 24 days. In contrast, afterripened seeds had 100% germination and mean germination times < 5 days at all incubation temperatures. Mean dormancy periods varied between 4 months and < 1 month, as negative linear or negative log-linear functions of storage temperature. Mean germination time was a negative linear function of months in storage; the slope of this relationship (coefficient of rate change) indicated how quickly mean germination times change during storage. For seeds stored at 10°C, coefficients of rate change were tightly clustered and only slightly negative; warmer storage generally resulted in faster acceleration of germination speed. Even after seeds were no longer dormant, mean germination times decreased with further storage. These findings indicate that while recently harvested cheatgrass seeds from contrasting habitats differ widely in their response

to incubation temperatures (i.e., they are dormant and slow to varying degrees), when afterripened they are similar (i.e., nondormant and fast).

Introduction

Cheatgrass (*Bromus tectorum* L., also June grass or downy brome), native to Eurasia, is a major invasive weed in semiarid ecosystems of the Western United States. Caryopses (hereafter seeds) of this exotic annual ripen in early to midsummer and exhibit varying degrees of dormancy at maturation (Beckstead, Meyer, and Allen, 1994; Milby and Johnson, 1987). Cheatgrass is facultatively fall-germinating. Seeds germinate in response to autumn rains (Milby and Johnson, 1987), postpone germination until winter or early spring, or carry seeds across years as components of the soil seed bank (Young et al. 1968; Hull and Hansen 1974). In order for fall germination to occur, the seeds must become nondormant through afterripening (i.e., loss of dormancy in dry seeds over time) and experience sufficent precipitation inputs to complete the germination process.

In order to accurately predict germination timing of cheatgrass, information regarding the germination behavior is necessary; in particular, a knowledge of intrinsic characteristics of the seed population upon dispersal, as well as changes in dormancy status and germination speed over a range of storage and subsequent incubation temperature regimes.

Previous studies on afterripening of cheatgrass (Milby and Johnson, 1987; Thill et al. 1980) did not include a wide range of both storage and incubation temperature regimes over which to characterize afterripening. This study was conducted to determine the relationship between storage temperature, storage duration, and incubation temperature for seed germination of three cheatgrass collections from contrasting habitats. The results presented in this paper are representative of data obtained from 20 cheatgrass accessions collected throughout the Intermountain West, and will be used to develop a descriptive model of the effects of temperature on afterripening and germination of cheatgrass seeds.

Methods

The experiment described was a complete factorial that included 3 collections, 4 storage temperatures, 5 storage durations, and 4 incubation regimes as described below. Fully mature seeds were hand-collected from three cheatgrass populations representing differing ecological habitats (Table 1). Within two weeks from the time of collection, seeds were cleaned and stored in sealed containers at constant temperatures of 10, 20, 30, and 40°C. Seed moisture contents ranged from 7 to 8% (dry weight basis) throughout storage. At monthly intervals from zero (recently harvested seeds) to four months, subsamples were removed and

germination tests performed. For each treatment, four replications of 25 seeds were placed in 100 X 15 mm plastic petri dishes on two germination blotters (Anchor Paper, St. Paul, Minnesota) kept saturated with tap water. Seeds were incubated under cool-white fluorescent lights (12:12 h light: dark cycle) at alternating temperature regimes of 5/15, 10/20, 15/25, and 20/30°C, with the higher temperature corresponding to the light period. Dishes were randomized, stacked, and placed in plastic bags to reduce water loss, with a blank dish (blotters but no seeds) on top of each stack. Germination (radicle emergence to 1 mm) was scored at 2, 4, 7, 11, 14, 21, and 28 days of incubation. Seeds remaining after 28 days were subjected to a cut test (Beckstead, Meyer and Allen, 1994) to determine viability. Viable, ungerminated seeds were classed as dormant.

Several germination indices were used to characterize the extent to which afterripening had occurred: percent germination during 28-day incubation; days required to reach 50% of total 28-day germination (Mean germination time) as an index of germination rate, and days between10% and 90% of 28-day germination (D_{90} -D_{10}) as an index of germination uniformity (Hardegree and Emmerech, 1992). Values for mean germination time and uniformity were determined by interpolating from rate curves. For each storage temperature X storage duration X incubation temperature treatment combination, the mean dormancy period (storage

time required for 1/2 of originally dormant seed fraction to become nondormant) was determined (Roberts 1962). Values for mean dormancy were obtained from probit transformations of curves plotting the dormancy loss (i.e., 28-day germination of originally dormant fraction) over time for each treatment combination. The probit transformation linearizes a cumulative normal distribution, which is characteristic of dormancy periods within a seedlot (Roberts, 1988).

Linear regressions of mean germination time on storage duration (0-3 months; all but the first mean germination time value below 5 days also excluded) were determined for each incubation temperature. As all regressions were significant ($p<.01$), the slope of this relationship was used as a coefficient of rate change to describe how quickly mean germination time changed during storage.

Germination percentages were converted to a percentage of viable seed basis to facilitate comparisons among sources. For each of the dependent variables (28-day germination, Mean germination time, and uniformity, results were analyzed as a completely randomized design using analysis of variance procedures. Percentage data were arcsine transformed for analysis. Differences among treatment means were evaluated using Student-Newman-Keuls means separation test.

Results

Because space limitations do not allow presentation of cumulative germination curves (n=240), generalized curves representing the range of observed responses are depicted in Figure 1. Curve A illustrates typical cumulative normal distribution for a seed lot with no dormant seeds. Germination is relatively rapid (low mean germination time) and uniform (low $D_{90} - D_{10}$). Curve B is similar to curve A except there is a longer lag phase before the onset of germination. This results in a larger mean germination time but similar uniformity. In curve (?) C, seeds are nondormant but do not follow a cumulative normal (double sigmoidal) distribution. Rather, sporadic germination leads to a response that is linear through time. In this example, mean germination time is similar to Curve B but germination is less uniform. Curve (?) D illustrates the case where half of the seeds do not germinate because they are dormant. Mean germination time and uniformity values are identical to C because they consider only the nondormant seed fraction. Note that D could also approximate a cumulative normal distribution as in A and B. A fifth possibility, not shown, applies to seed lots that are 100% dormant and therefore do not germinate. As described below, germination of recently harvested seeds approximated curve D; as afterripening continued, cumulative germination progressively approached curve A.

8The major purpose of this literature

Populations of recently harvested cheatgrass seeds had a considerable dormant fraction at all incubation temperatures (Figure 2). At this stage, percent germination ranged from 17-24% for Whiterocks, 27-72% for Hobblecreek and 1-64% for Green River, depending on incubation tamperature. The ANOVA run on combined accessions showed that maximum germination percentages for recently harvested seeds occurred at 10/20°C, although the difference between bordering regimes was significantly different only for the Green River source when the ANOVA was run separately on each collection. Seeds from Whiterocks were highly dormant at all incubation temperatures. Germination of Green River seeds was strongly temperature dependent; more than half of the seeds germinated at 10/20°C but almost no seeds germinated at 20/30°C. Hobblecreek, which was the least dormant source, also showed strong temperature inhibition at high temperatures.

Essentially all seeds were nondormant following four months of storage at 40 (Figure 2), 30, and 20°C (not shown). Seeds had not completely lost dormancy at10°C storage for four months, where incubation at 20/30°C resulted in germination of 37, 66, and 44% for White Rocks, Hobblecreek and Green River, respectively.

In general, mean dormancy period was negatively correlated with storage temperature and positively correlated with incubation

temperature (Figure 3). This is most evident with Green River seeds, which showed a negative loglinear relationship between mean dormancy period and stoarage temperature at the two highest incubation temperatures, and a linear relationship at the two lowest incubation temperatures (graph shown utilizes linear scale). Studies with rice (Roberts 1962, 1965) demonstrated that the relationship between storage temperature and mean dormancy period was a negative loglinear function of storage temperature. This has subsequently been shown with other grasses as well (Roberts and Smith, 1977; Stoanova and Kostov, 1983; Stoanova et al. 1984). Because we did not sample between between 0 and 1 month storage, our data for low incubation temperatures do not preclude the possibility that the relationship is indeed nonlinear. Certainly, it appears that for Hobblecreek and Green River, a loglinear relationship may apply. Whiterocks, which had a high degree of dormancy with little temperature sensitivity (Figure 1), has tightly clustered mean dormancy period values with multiple crossovers. While afterripening is more rapid at high storage temperatures, the effects of incubation temperature are less consistent for this source. In contrast, the two temperature sensitive sources had the lowest mean dormancy periods when incubated at the lower temperature regimes.

In addition to a decline in the dormant fraction, afterripening results

in substantially reduced mean germination times (Figure 4). These values ranged betwen 10 and 24 days for recently harvested seeds, but had dropped to less than five days for afterripened seeds. In general, cheatgrass seeds germinated most rapidly at the lowest incubation temperature when recently harvested, but were slowest at this temperature when afterripened. In evaluating changes in mean germination time, note that the fraction of seeds being considered varies considerably (Figure 1). For example, Figure 4 illustrates that recently harvested Green River seeds had mean germination times between 14 and 18 days. However, this value is based on drastically different fractions of the seed population (64% at 10/20°C but only 1% at 20/30°C incubation).

Strong between-collection differences were observed with respect to changes in rate and dormancy. Comparing Figures 2 and 4 illustrates that for White Rocks, germination percentage of fresh seeds was not affected by incubation temperature, while mean germination time increased approximately linearly with temperature. In contrast, percent germination of Green River seeds was strongly affected by incubation temperature, while mean germination times were similar for all incubation temperatures. Both percentage germination and mean germination time were strongly affected by incubation temperature for Hobblecreek seeds. Seeds stored for four months at 40°C take longer to germinate at 5/15°C

than at higher temperatures (Figure 4). This is due to a lower maximum germination speed at this temperature, and not because seeds had not afterripened fully. Even after 17 months storage (data not shown), mean germination times did not increase for 5/15oC incubation.

A negative linear relationship can be used to describe reduction of mean germination time during storage (Figure 5). Regressions of months in storage on mean germination time were highly significant ($p<.01$). The slope of resulting regression lines plotted against storage temperature was used as a coefficient of rate change to describe how rapidly mean germination times decreased during storage (Figure 6). Values were less negative and tightly clustered with 10oC storage and diverged as storage temperature increased. At 10/20 C incubation, there was no difference between storage at 30 and 40oC, or at 20oC except for Green River. At 5/15oC, mean dormancy period changed very little with storage at any temperature. For Whiterocks and Hobblecreek, the strongest storage temperature dependence was observed with 15/25 and 20/30oC incubation. For Green River, however, germination was inhibited by high temperature incubation until after two months of storage; therefore, a low coefficient of rate change was observed. Prolonged inhibition at high incubation temperature also accounts for the crossovers observed at 20/30oC incubation between 30 and 40oC storage. Because afterripening

occurred more rapidly at 40oC, the inhibitory effects of high temperature incubation were overcome more quickly; therefore, seeds reache the maximum germination speed more rapidly at this storage temperature. Where high imbibition temperature inhibition was not a confounding factor, highly negative coefficients of rate change were largely a reflection of how slow recently harvested seeds germinated for a particular treatment.

Seeds germinated much more uniformly as a result of afterripening (Figure 7). For recently harvested seeds, there was a trend for higher D_{90}-D_{10} values (i.e., decreased uniformity) when seeds were incubated at 10/20oC, even though this temperature resulted in the maximum 28-day germination (Figure 2). Incubation above and below this temperature resulted in lower 28-day germination, but germination tended to occurr

Discussion

Recently harvested cheatgrass seeds have a degree of seed dormancy, and germinate slowly and asynchronously (Figure 1, Curve D). These characteristics are strongly influenced by incubation temperature and vary among seed collections. Differences among collections have ecological significance that are not discussed here (Beckstead, Meyer and Allen, 1994). Inherent differences among mature seeds in a single

population as well as between populations leads to a wide range of responses upon incubation under different temperature regimes. While slow germination is often interpreted as indicative of low vigor for agronomic speices (e.g., Steiner,1990), this is clearly not the case for unafterripened seeds. Studies involving over 50 seedlots of barley showed that lots with high dormancy are characterized by germination that is slow at low incubation temperatures and inhibited at high incubation temperatures (Ellis et al. 1987).

Dry storage resulted in progressively greater germination percentages during incubation, as well as germination that was progressively faster and more uniform. Therefore, optimum conditions (i.e., resulting in rapid, uniform germination of the maximum germination percentage) include the lower temperature regimes initially, but expand to include the highest temperature regime over time.

Changes in dormancy fraction are not analogous to changes in germination speed. Even after all dormancy is lost (i.e., seeds willl germinate in 28 days), mean germination time continues to decrease with further storage. The use of 28-day incubation as the cutoff for defining germination, though common (Young and Evans, Ellis et al. 1987), is arbitrary. Ellis et al. (1987) showed that the dormant fraction of unafterripened barley seedlots germinated sporadically during nine

months of continuous incubation. In our study, the effect of progressively reducing the incubation test period would be a progressive increase in dormancy fraction coupled with a progressive loss of ability to resolve changes in germination speed. For example, with the extreme case of an incubation period less than 5 days, all lots in this study would have been scored as completely dormant initially, and differences in germination speed completely obscured. While almost no published reports deal with changes in rate during afterripening (Ellis et al. 1987, Milby and Johnson, 1987 are exceptions), increased germination speed should be recognized as an important change associated with afterripening.

Mean germination times for recently harvested cheatgrass seeds were greater than 10 days, even at low incubation temperatures (Figure 4). Thus, only a fraction of unafterripened seed is germinable, and this fraction germinates slowly. Lengthy requirement for continuous hydration would greatly reduce the possibility for field germination of unafterripened seeds in semiarid habitats, because soils do not remain moist for a sufficient time period to complete the germination process. While related studies have demonstrated that grass seeds can accumulate progress toward germination over a series of hydration-dehydration cycles (Allen et al. 1993; Allen et al. 1994), precipitation data for the sites used in this study (ONOAA, 1974; S. Meyer, unpublished data) indicate that it is

unlikely that a large fraction of these seed populations could germinate during summer months before appreciable afterripening had occurred. A given precipitation event would therefore elicit a different germination response if it occurred in summer (unafterripened seeds) than in the fall (unafterripened seeds), even if coupled with identical soil temperature and moisture regimes. In summer, time seeds spent hydrated would result in progress toward germination, but at a rate so slow that only a small fraction of the seed population, if any, could complete radicle emergence. Identical temperature and moisture conditions in the fall would trigger germination of a much larger seed fraction. Thus, time seeds spend in the hydrated state is relative to the degree of afterripening that has occurred as well as the inherent seed status at maturity.

Table 1. Habitat information* for cheatgrass collection sites

Location	Elevation (m)	Mean June Maximum Temperature (C)	Mean Annual precipitation (cm)	Habitat Type
Whiterocks, Utah	1450	29	18	cold desert
Hobblecreek, Utah	1811	22	51	mountain brush
East Green River, Utah	1280	32	13	salt desert

*References: Stevens et al. (1983); United States Department of Commerce (1974)

Legends for Figures 1-7.

Figure 1. Generalized range of observed responses in 240 afterripening treatments. Cumulative germination curves are discussed in text.

Figure 2. Germination percentages for recently harvested and afterripened cheatgrass seeds following 28-day incubation. All values for recently harvested seed are significantly different ($p < .05$) from those for seeds stored four months at 40°C. For each line, values associated with the same letter are not significantly different ($p < .05$) as determined by Student-Newman-Keuls test.

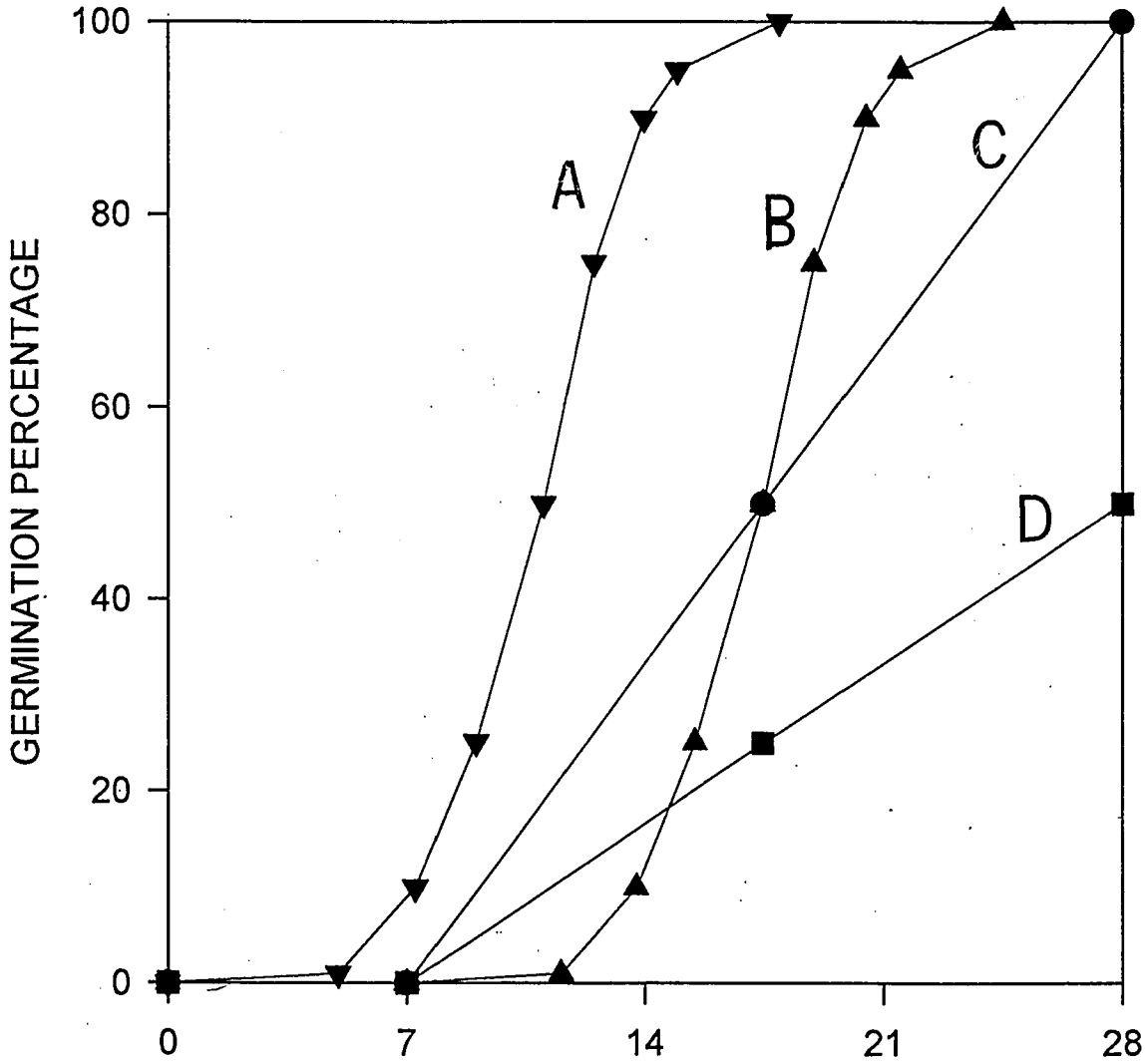
Figure 3. The effect of storage and incubation temperatures on mean dormancy period.

Figure 4. Mean germination times for recently harvested and afterripened cheatgrass seeds following 28-day incubation. All values for recently harvested seed are significantly different ($p < .05$) from those for seeds stored four months at 40°C. For each line, values associated with the same letter are not significantly different ($p < .05$) as determined by Student-Newman-Keuls test.

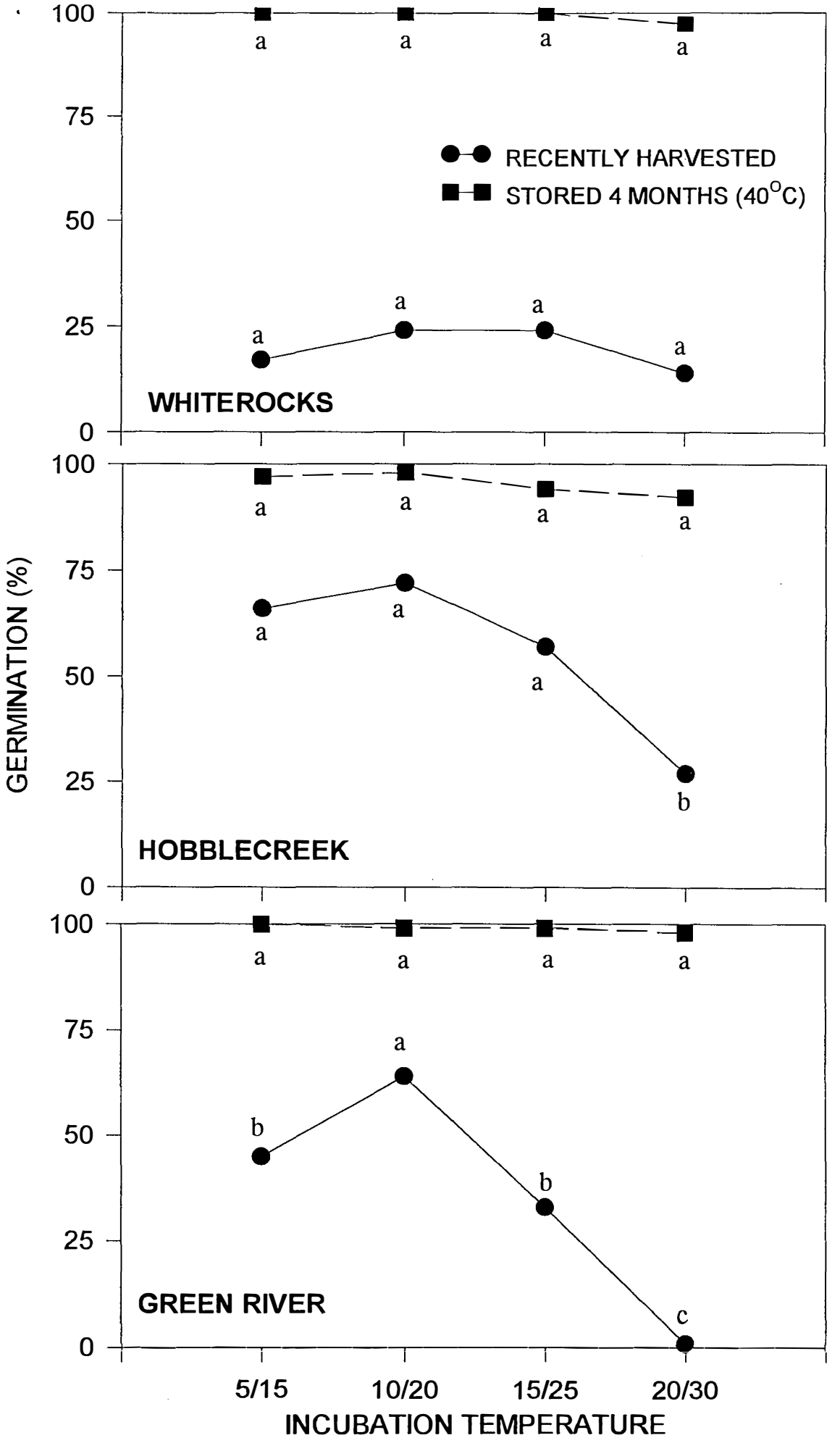
Figure 5. The effect of storage temperature on mean germination time for Hobblecreek cheatgrass seeds incubated at 20/30°C. All regression lines are significant ($p<.05$).

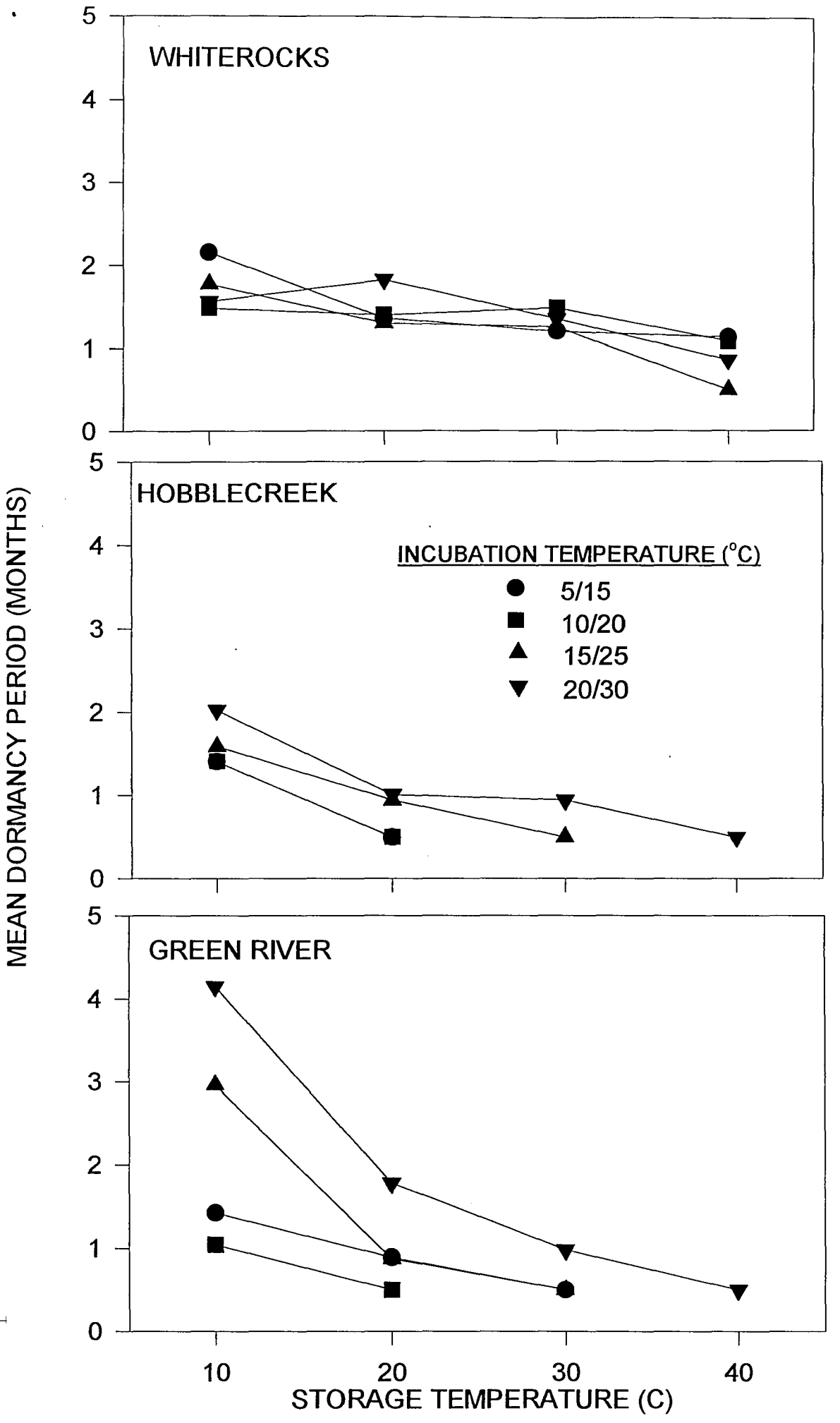
Figure 6. The effect of storage and incubation temperatures on coefficient of rate change (slope of of mean germination time regressed on months in storage).

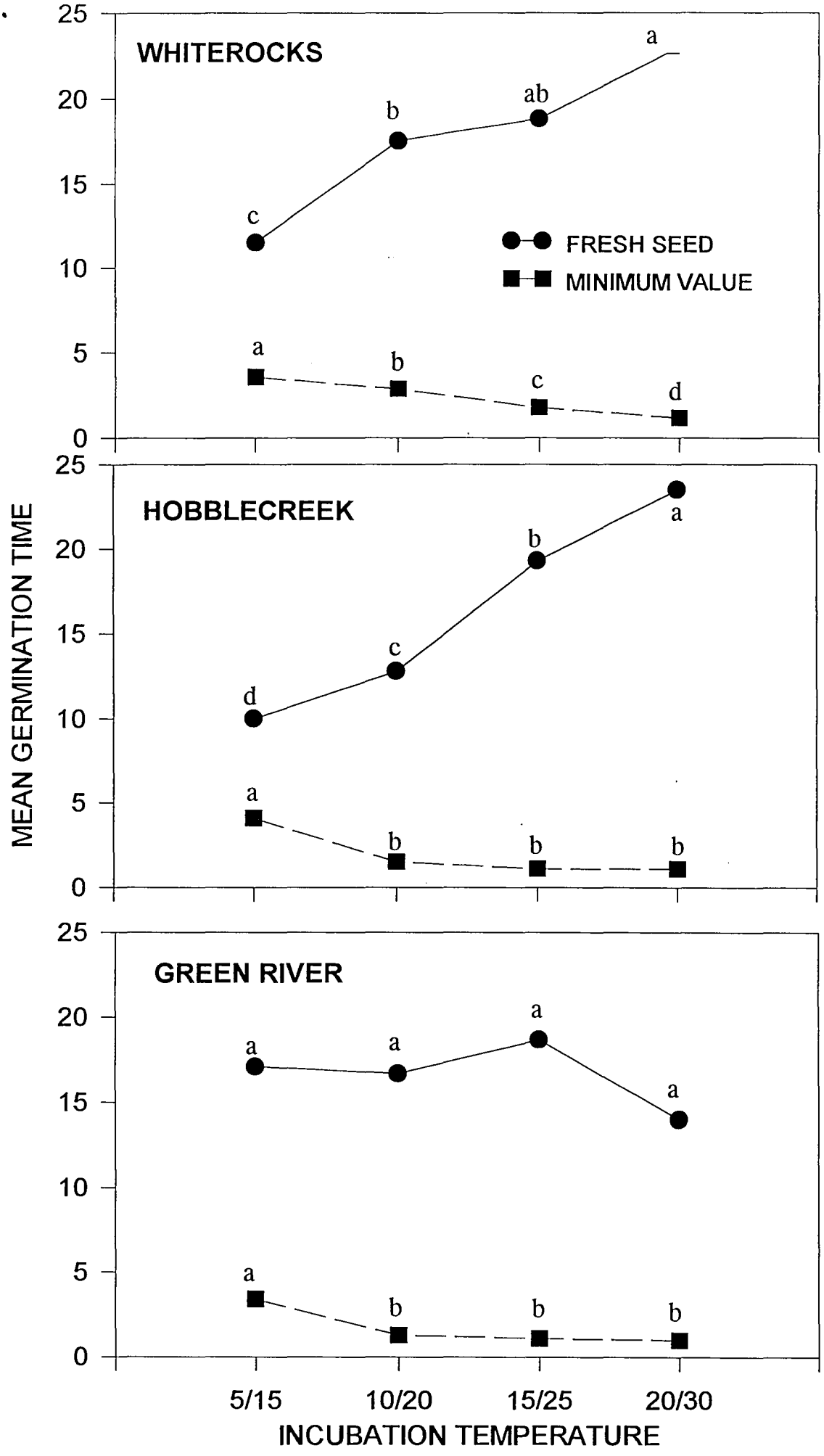
Figure 7. Uniformity of germination for recently harvested and afterripened cheatgrass seeds during 28-day incubation. All values for recently harvested seed are significantly different ($p <.05$) from those for seeds stored four months at 40°C. For each line, values associated with the same letter are not significantly different ($p<.05$) as determined by Student- Newman-Keuls test.



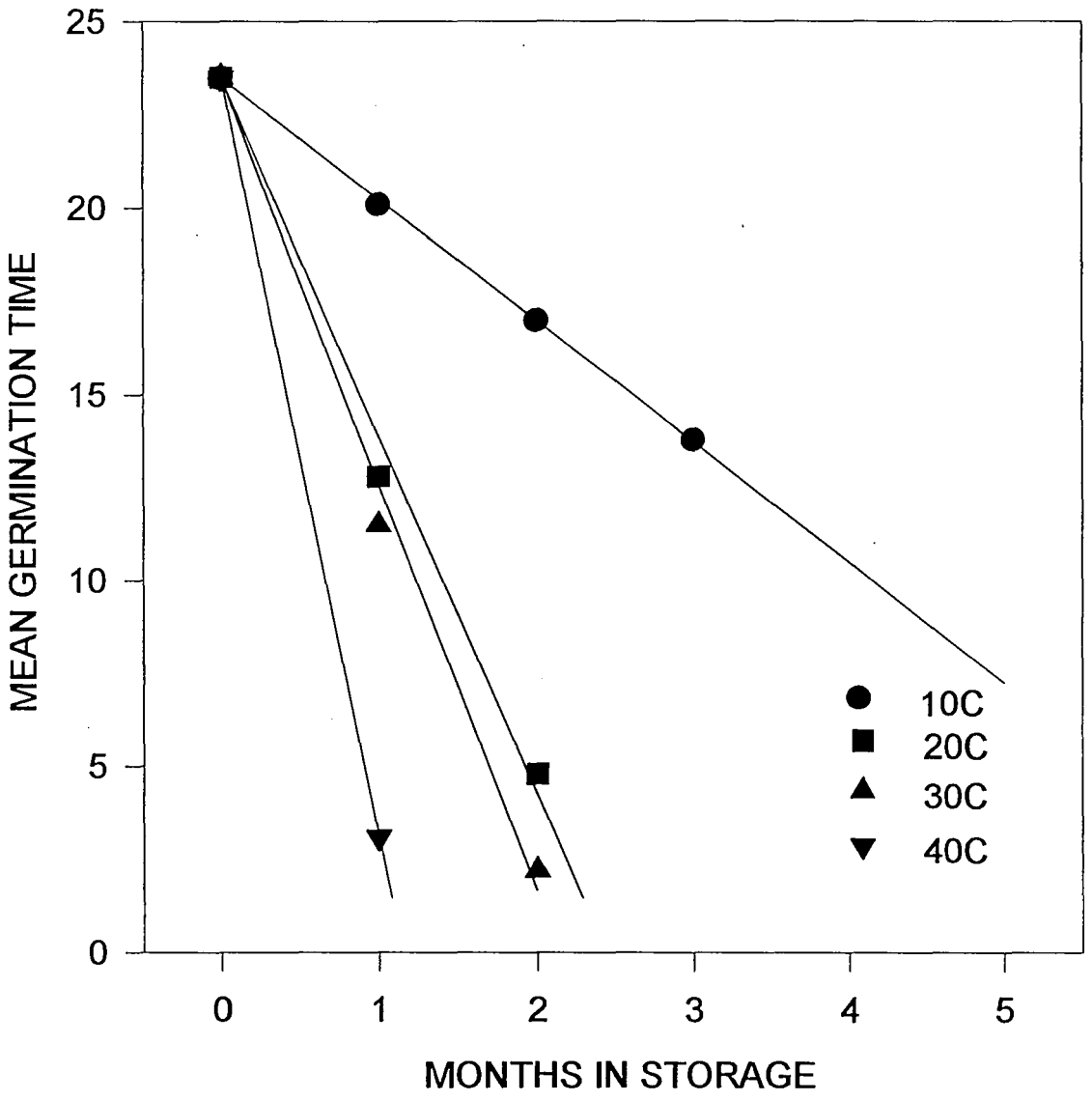
CURVE	PGERM (%)	T_{50} (DAYS)	ISYNCH (T_{90}-T_{10})
▼—▼	100	11	6.8
▲—▲	100	17.5	6.8
●—●	100	17.5	16.8
——	50	17.5	16.8

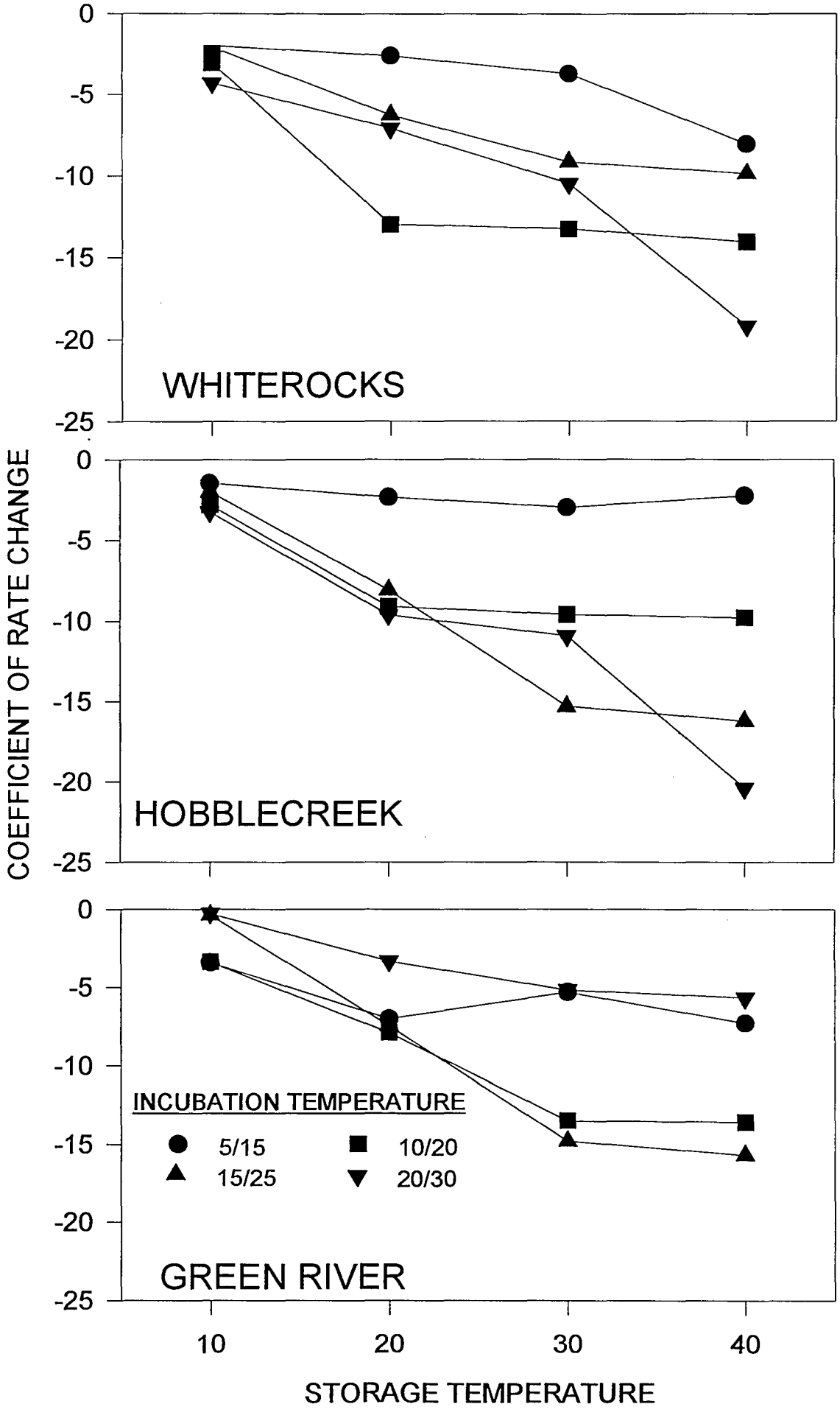

GERMINATION (%)
100
75
50
25
0
RECENTLY HARVESTED
STORED 4 MONTHS (40°C)
WHITEROCKS
HOBBLECREEK
GREEN RIVER
5/15
10/20
15/25
20/30
INCUBATION TEMPERATURE

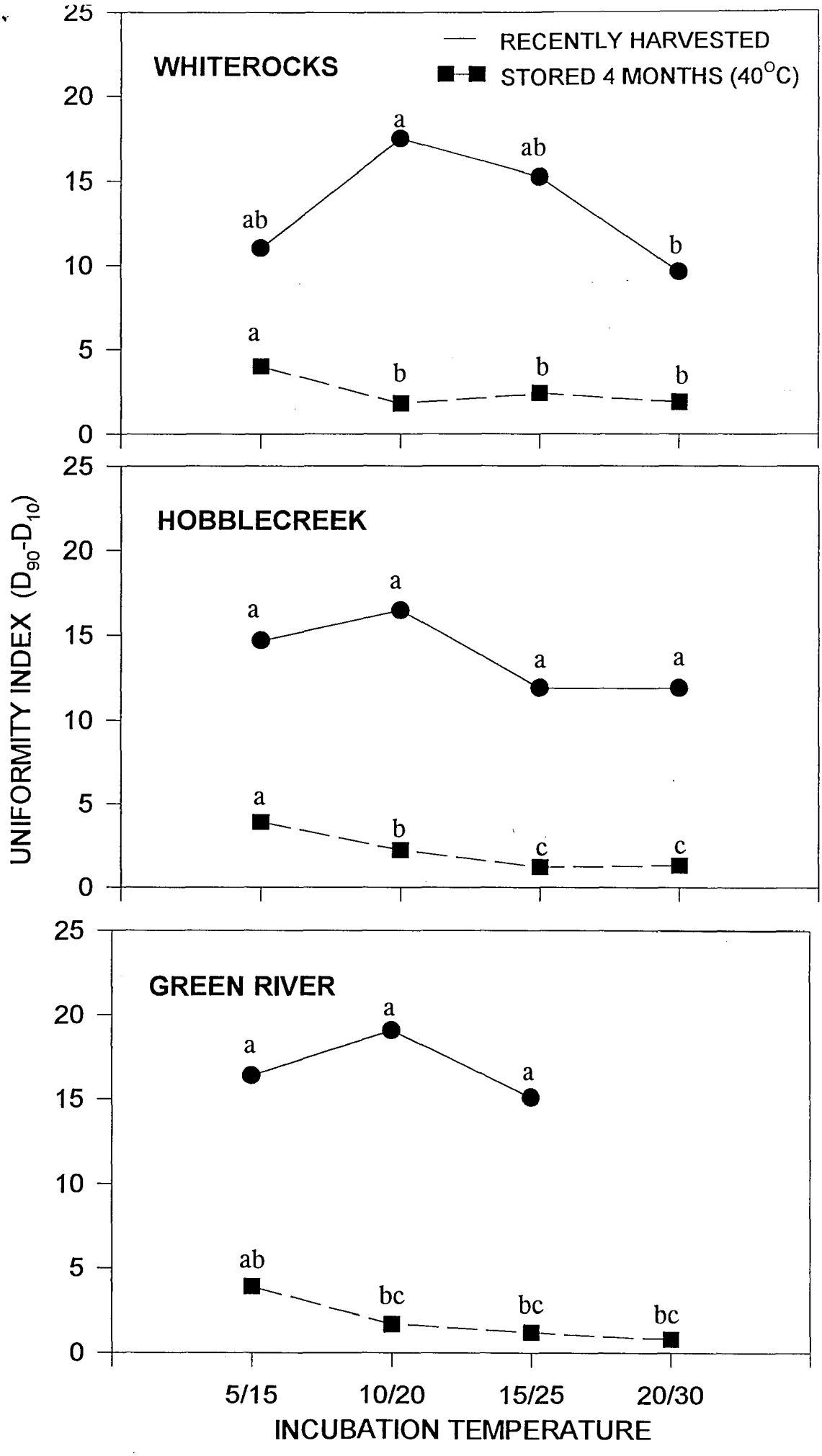

WHITEROCKS
HOBBLECREEK
GREEN RIVER
INCUBATION TEMPERATURE (°C)
5/15
10/20
15/25
20/30
MEAN DORMANCY PERIOD (MONTHS)
STORAGE TEMPERATURE (C)
0
1
2
3
4
5
10
20
30
40


WHITEROCKS
HOBBLECREEK
GREEN RIVER
FRESH SEED
MINIMUM VALUE
MEAN GERMINATION TIME
INCUBATION TEMPERATURE
5/15
10/20
15/25
20/30
0
5
10
15
20
25

HOBBLECREEK (20-30C INCUBATION)




0
-5
-10
-15
-20
-25
WHITEROCKS
HOBBLECREEK
GREEN RIVER
COEFFICIENT OF RATE CHANGE
INCUBATION TEMPERATURE
5/15
10/20
15/25
20/30
10
20
30
40
STORAGE TEMPERATURE


WHITEROCKS
RECENTLY HARVESTED
STORED 4 MONTHS (40°C)
HOBBLECREEK
GREEN RIVER
UNIFORMITY INDEX (D90-D10)
INCUBATION TEMPERATURE
5/15
10/20
15/25
20/30
0
5
10
15
20
25
a
ab
b
c
bc

A Comparison of the Effects of Afterripening on Cheatgrass (Bromus tectorum) and Squirreltail (Elymus elymoides) Germination

Julie Beckstead, Susan E. Meyer, and Phil S. Allen[1]

Abstract

Cheatgrass or downy brome (Bromus tectorum), an exotic facultatively fall-germinating annual, is displacing native plant communities throughout the Intermountain West. Squirreltail (Elymus elymoides), a native facultatively fall-germinating perennial, can reestablish naturally in rangelands infested by cheatgrass. This study was conducted to determine whether cheatgrass and squirreltail afterripen during dry storage in preparation for possible fall-germination and to compare between-population differences in response to afterripening. Seeds of four populations of each species were stored at 0, 10, 20, 30, and 40ºC over a period of four months and then incubated at

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[1] Paper presented at the Symposium on Wildland Shrub and Arid Land Restoration, Las Vegas, NV, October 19-21, 1993. This research was supported in part by funds provided by the Intermountain Research Station, Forest Service, U.S. Department of Agriculture.

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four temperature regimes. Afterripening in dry storage resulted in complete loss of dormancy and faster germination. In general, afterripened squirreltail collections never germinated as rapidly as cheatgrass. Between-population differences in afterripening patterns were habitat-correlated and ecologically relevant. Artificial seed bank experiments showed that both species fall emerge, although cheatgrass consistently germinated earlier than squirreltail. Our results indicate that both species afterripen in dry storage; this can permit fall-germination when it is advantageous for survival. Early fall seeding of squirreltail into cheatgrass-infested rangelands could be effective in future restoration projects.

Introduction

Cheatgrass or downy brome (*Bromus tectorum*; Poaceae) was introduced into the Intermountain West through contaminated grain from Eurasia in the late 1800's. Deteriorating range conditions in the early 1900's fostered the initial invasion and widespread establishment of this exotic weed (Mack 1981). Cheatgrass is an effective competitor for soil water resources, thus enabling it to infest the more arid regions of Washington, Idaho, Oregon, Nevada, Utah, and British Columbia. Currently

it is displacing various native plant communities. Billings (1990) reports that millions of acres of sagebrush and pinyon-juniper are now dominated by cheatgrass. Other habitat types invaded by cheatgrass include salt desert shrub, mountain brush, and some mountain meadows. Studies also show that cheatgrass invasion has increased frequency and intensity of fires in the Intermountain West, thus disrupting the entire natural ecosystem (Whisenant 1990). Overall, invasion by cheatgrass and associated fires affect at least 40 million hectares, making this perhaps the most significant plant invasion in North America (D'Antonio and Vitousek 1992). Thus, restoration of lands dominated by cheatgrass has become an important issue in the Intermountain West.

Squirreltail (*Elymus elymoides*; Poaceae; previously *Sitanion hystrix*) is a native perennial bunchgrass to the Intermountain West. It is a natural invader of disturbed areas in deserts, valleys, foothills, and mountain meadows. Squirreltail can reestablish naturally in rangelands infested by cheatgrass and medusahead (Hironaka and Sindelar 1973). Therefore, squirreltail is a logical native species to examine for possible restoration of degraded rangelands. Prior to understanding the successful long term persistence of cheatgrass and the ability of squirreltail to reestablish in cheatgrass-infested rangelands, the

germination strategies of both species must be considered.

Cheatgrass and squirreltail have both similarities and differences in their plant life histories with respect to reproduction and establishment. Cheatgrass is an exotic winter annual which facultatively fall-germinates; squirreltail is a perennial bunchgrass which is also known to facultatively fall-germinate (Hironaka and Sindelar 1973). Squirreltail, like cheatgrass, flowers in spring or early summer. Seeds of both species from lower elevation populations mature in early June while seeds from high montane populations do not ripen until late July. Dispersal occurs a few weeks following seed maturation. While cheatgrass seeds are dispersed via attachment to animals over long distances or by wind over short distances, squirreltail seeds are dispersed primarily via wind. As an annual, cheatgrass relies entirely on seeds for population replacement and invasion of new habitats. As a nonclonal perennial, squirreltail relies on seeds for population expansion as well as invasion of new habitats.

Cheatgrass and squirreltail, like many summer-ripening and facultatively fall emerging species, have safeguards against precocious summer germination (i.e., seed dormancy and/or slow germination) and lose these protective mechanisms through afterripening. A variety of definitions of afterripening are used in the literature (Vegis 1964;

Taylorson and Brown 1977; Baskin and Baskin 1986), but for the purpose of this paper, afterripening will be defined as a process that takes place in dry seeds and results in a reduction of dormancy and/or decrease in mean germination time (i.e., days to 50% germination). In other words, afterripening is the mechanism by which fall germination becomes possible.

There are conflicting reports concerning the afterripening of cheatgrass and squirreltail. Most studies involved investigations of only one plant population per species. Young and Evans (1977) suggested that cheatgrass and squirreltail seeds do not have afterripening requirements dependent on temperature. Other researchers, however, have shown that afterripening is often a characteristic of fall germinating grass species (Laude 1956; Taylorson and Brown 1977; Thill and others 1980; Baskin and Baskin 1986). Afterripening at high storage temperatures has been found to occur in cheatgrass, reducing the initial level of dormancy (Laude 1956; Thill and others 1980) and decreasing the mean germination time (Milby and Johnson 1987). A variety of grass seeds showed increased germination percentage when stored at 50°C for 14 days (Taylorson and Brown 1977). Afterripening not only increased seed germination percentage, but also the temperature range over which seeds could

germinate (Thill and others 1980; Baskin and Baskin 1989). Research published to date on cheatgrass and squirreltail does not contain a consensus as to whether seeds of these species afterripen.

The objectives of this study were to: (1) determine whether cheatgrass and squirreltail seeds afterripen during dry storage; (2) investigate the effects of storage and incubation temperature on germination percentage and mean germination time (i.e., days to 50% germination); (3) relate changes in the mean germination time to species and habitat; and (4) evaluate fall germination of cheatgrass and squirreltail through artificial field seed bank experiments.

Materials and Methods

Afterripening Storage Treatments

Mature fully ripened seeds (caryopses with associated lemma and palea) were hand-stripped from four populations each of cheatgrass and squirreltail in the summer of 1992. Collections were cleaned using a rubber seed cleaning board and a small fanning mill. Seeds were then hand-selected to improve fill. Collection sites represented four distinct habitats; two low elevation sites, consisting of cold desert and salt desert and two high elevation sites, consisting of mountain brush and

mountain meadow (Table 1). Elevation was determined from topographic maps for each collection site.

Storage

Within two weeks of harvest, seeds (7-8% moisture content) underwent controlled dry storage treatments. Squirreltail seeds were stored at 0, 10, 20, 30, and 40°C for 12 weeks. Cheatgrass seeds were also stored at 0, 10, 20, 30, and 40°C, except for mountain brush and mountain meadow collections, which were stored at 0, 20, and 40°C only.

Incubation

Germination experiments were conducted at the initiation of storage treatments (recently harvested seeds) and at 4-week intervals thereafter. For each species collection and storage temperature treatment, four replications of 25 seeds were placed in 100 x 10 mm plastic petri dishes on two germination blotters (Anchor Paper, St. Paul MN) saturated with tap water. Petri dishes were grouped and randomly stacked in plastic bags closed with rubber bands to retard water loss. Dishes were rewetted as needed. A blank dish was placed on each stack to ensure that all dishes received equal light. Dishes were incubated in controlled-environment chambers under cool-white fluorescent lights with a 12-hour photoperiod. Temperatures corresponded to possible field temperatures for

germination: 5/15, 10/20, 15/25, and 20/30°C. Seeds were classified as germinated when the radicle had elongated to 1 mm. Dishes were inspected for germination on days 2, 4, 7, 11, 14, 21, and 28 following the onset of incubation. Dormant seeds were defined as seeds that did not germinate within 28 days, but were viable. At the end of the 4-week incubation period, viability of ungerminated seeds in each dish was determined using a cut test. A cut test examines the seed tissue. Fully developed, firm tissue with the proper coloring is considered viable while shriveled, decayed, and discolored tissue or seed lacking an embryo is considered nonviable (Association of Official Seed Analysts 1988).

Germination percentage (viable seed basis) and mean germination time (calculated as days to 50% of total germination) were determined for each replication. Analysis of variance (ANOVA) was used to test for the effects of species, habitat type, storage temperature, storage duration, and incubation temperature. Linear regression was used to examine progressive changes in mean germination time as a function of storage duration for each collection x storage temperature x incubation temperature combination.

General weather information for each seed collection site was examined to evaluate conditions seeds naturally undergo during ripening

and following dispersal. Mean monthly temperature and monthly precipitation were obtained for each collection by interpolating on isotherm maps, supplemented with information from nearby weather stations when available (Water Information Center 1974; Stevens and others 1983).

Artificial Seed Bank Experiment

Artificial field seed bank experiments were carried out with two of the four cheatgrass collections and three of the four squirreltail collections. Prior to placement in the field experiment, seeds were stored at 20°C. Groups of approximately 100 seeds (determined by weight) were placed in flat nylon mesh packets. In mid-August, the packets were buried at a depth of 0.5 cm with the exception of the squirreltail strawberry collection which was buried in mid-September. Each group of packets was protected with a hardwarecloth cone. Cones were arranged in three blocks at each of three field sites: a cold desert site (Whiterocks), a mountain brush site (Point of the Mountain), and a high elevation mountain meadow site (Strawberry) (Table 2). At monthly intervals through mid-November, mid-March (mid-May at Strawberry), and mid-June, three sets of packets were retrieved from each site and transported to the laboratory in an insulated chest on ice at 1°C. Within 6 hours, germinated seeds in each

packet were counted, and remaining seeds were placed in petri dishes, incubated at 10/20°C for four weeks, and scored at least weekly for germination as described previously. Seeds that germinated during post-field incubation were classified as ungerminated but laboratory-germinable, while any viable seeds remaining at the end of four weeks were classified as dormant.

Results

Afterripening Storage Treatments

Storage temperature and duration had a dramatic effect on both germination percentage and mean germination time. Recently harvested seeds (before afterripening storage treatments) showed some dormancy and germinated slowly. Fully afterripened seeds became nondormant and germinated much faster than recently harvested seeds (Table 3).

Although, recently harvested cheatgrass and squirreltail collections showed dormancy, squirreltail was less dormant than cheatgrass. Following the dry afterripening treatment, cheatgrass and squirreltail seeds for all collections reached 100% germination. Recently harvested cheatgrass and squirreltail collections showed a relatively long mean germination time in contrast to a shorter mean germination time for the

fully afterripened seeds. Squirreltail collections never germinated as rapidly as cheatgrass.

Recently harvested desert collections had higher levels of dormancy than did the mountain collections. Fully afterripened seeds from all habitats became nondormant. All habitats germinated faster when fully afterripened, although the mountain meadow population had the slowest germination.

Incubation Temperature Effects

The optimum incubation temperature for recently harvested seeds for both germination percentage and time was 10/20°C (Table 3). The least optimal incubation temperature for recently harvested seeds for germination percentage and time was 20/30°C. However, when seeds were fully afterripened the optimum incubation temperature for mean germination time occurred at 20/30°C. All fully afterripened collections became completely nondormant and unrestricted across the tested range of incubation temperatures.

Recently harvested cold desert and salt desert cheatgrass populations were quite dormant and germination was restricted at some incubation temperatures (Figure 1). Furthermore, salt desert cheatgrass germination was extremely restricted at both 15/25 and 20/30°C. In

contrast, the recently harvested cold desert and salt desert squirreltail populations showed less restriction in germination, although dormancy was greatest at 20/30°C for the cold desert squirreltail and at both 5/15 and 20/30°C for the salt desert squirreltail. Recently harvested mountain cheatgrass and squirreltail populations showed less dormancy than the desert populations. Mountain squirreltail collections were less dormant than mountain cheatgrass collections at high incubation temperatures. Mountain cheatgrass dormancy was most pronounced at 20/30°C; whereas, mountain squirreltail dormancy was most pronounced at 5/15°C.

Mean germination time of fully afterripened seeds was higher than that of recently harvested seeds for all incubation temperatures for both species (Figure 2). The optimal incubation temperature for fast germination was reversed as a result of afterripening for cheatgrass collections. While recently harvested cheatgrass seeds germinated fastest at 5/15°C, fully afterripened seeds germinated fastest at 20/30°C. Squirreltail populations did not reverse optimal incubation temperature following storage. Afterripened squirreltail populations had a more rapid germination, but not to the extent of the cheatgrass populations. However, recently harvested squirreltail seeds did show a higher initial germination time across the incubation temperatures.

Storage Temperature Effects

Comparing changes in mean germination time across weeks in dry storage revealed clear patterns for both species. Cold desert (Figure 3) and mountain meadow populations (Figure 4) represented the two extreme habitat types. The mean germination time changed less at incubation temperatures of 5/15 and 10/20°C than the mean germination times at 15/25 and 20/30°C for both habitat types. In general, the negative relationship between mean germination time and weeks in dry storage for each collection was significant ($p<0.05$) at 10, 20, 30, and 40°C storage temperatures. Changes during storage at 0°C usually were minimal, and changes in mean germination time became greater at higher storage temperatures. The mountain cheatgrass and squirreltail populations are an exception to this pattern; 40°C storage resulted in minimal or increased germination time. This effect was possibly due to loss of vigor resulting from storage at high temperature for an extended period, conditions unlikely to be experienced by mountain populations. Comparing habitat types, mountain populations showed less change in mean germination time following afterripening than desert populations. Change was most pronounced in cheatgrass populations, although, squirreltail cold desert populations also showed a slight change in mean germination time.

Artificial Seed Bank Experiment

Results from the artificial seed bank experiments showed that both species do facultatively fall-germinate (Figure 5). At the cold desert Whiterocks site, both cheatgrass collections reached 100% germination by mid-November, but only the S. Price squirreltail collection germinated (60%) by this time. The other two squirreltail collections postponed germination until late winter. When packets were excavated from beneath the snow in mid-March, squirreltail germination percentages ranged from 80% for the Strawberry collection to 98% for the S. Price collection.

At the mountain brush Point of the Mountain site, both cheatgrass collections had reached between 70% (E. Green River) to 90% (Whiterocks) germination by mid-September. By mid-November cheatgrass collections reached 100% germination. All three squirreltail collections reached 100% germination by mid-November, although there was no field germination prior to the mid-November retrieval excavation.

At the mountain meadow high elevation Strawberry site, by mid-September the E. Green River collection had reached 50% germination and the Whiterocks collection reached 90% germination. By mid-November both cheatgrass collections reached 100% germination. Only one squirreltail collection had germinated by mid-November (S. Price, 50%).

All the other squirreltail collections postponed germination until late winter. When packets were excavated from beneath the snow in mid-May, squirreltail germination percentages ranged from 80% for the S. Price collection to 100% for both the E. Salina and Strawberry collections.

Discussion

Completion of afterripening can be marked by reduction in dormancy and faster germination (Thill and others 1980; Milby and Johnson 1987). Populations of cheatgrass and squirreltail are at least conditionally dormant when recently harvested and respond to the afterripening treatments by reaching 100% germination, indicating that both species afterripen in dry storage. However, a reduction in dormancy is not the only factor influencing the probability of fall germination; a change in mean germination time is also necessary. Our results show that mean germination time decreased for both cheatgrass and squirreltail from 13.4 to 4.4 days following afterripening. The afterripening mechanism protects seeds from precocious summer germination but allows for fall-germination (Milby and Johnson 1987). The results of afterripening are clearly indicated by a reduction in dormancy and a decrease in mean germination time; however, mechanisms controlling afterripening are still

not fully understood.

Germination of recently harvested squirreltail seeds occurs primarily at moderate incubation temperatures (10/20 and 15/25°C), while higher incubation temperatures (20/30°C) inhibit germination. An examination of desert weather patterns (Figure 6) shows that in June and July, when field dispersal occurs, it is unlikely that seeds will experience temperatures of 10/20 and 15/25°C in combination with adequate moisture. In contrast, mountain sites may experience these temperatures in July. However, mountain-collected seeds ripen much later than the desert populations. The critical point is that the recently harvested seeds were dormant at 20/30°C incubation temperature, which represents conditions seeds will likely experience during June and July. Furthermore, recently harvested squirreltail populations show a long mean germination time (11.3 days). Therefore it is unlikely that squirreltail seeds would germinate precociously in the early to mid-summer.

The annual species, cheatgrass, germinates faster than squirreltail, a perennial. From an ecological stand point, this implies that cheatgrass benefits more from early fall germination than does squirreltail. This maybe due to the total plant reproductive output which is directly affected by fall germination and subsequent spring seed production for the

annual species (Mack and Pyke 1983). The lifetime reproductive output of squirreltail, a perennial, is probably not as dependent on emergence time, because plants will have more than one season to produce seed.

Recently harvested seeds from desert populations of both cheatgrass and squirreltail show more dormancy than mountain populations. This difference can partly be explained by the weather data, which show that the earlier ripening desert populations, experience a longer period of warm and relatively dry weather before conditions are suitable for fall germination (Figure 6). In contrast, mountain populations which ripen later have a relatively shorter period to wait for fall germination.

Precipitation, a limiting resource in the desert, is received principally in the winter, thus providing seedlings with adequate moisture for growth and increasing the probability of survival. Seedlings in a desert environment face a lower risk of winter mortality following fall emergence. The fact that desert populations show a greater change in the mean germination time in comparison to the mountain populations suggests that fall germination is of more importance to desert populations.

Low incubation temperatures were optimal for recently harvested cheatgrass and squirreltail germination (i.e., germination percentage and

mean germination time), whereas the high incubation temperatures were optimal for fully afterripened seed. This study supports others (Thill and others 1980; Baskin and Baskin 1989) in demonstrating that afterripening broadens the incubation temperature range at which germination occurs. In addition, the change in the mean germination time across weeks of storage was greater at higher incubation temperatures (20/30°C).

The artificial seed bank experiment indicates that both species can fall emerge in years of above-average autumn precipitation (such as occurred in 1992). All cheatgrass populations germinated completely by mid-November at all three field sites. Squirreltail populations fall-germinated completely at the mountain brush site, and partially at the other two sites. Cheatgrass consistently germinated earlier than squirreltail.

Results from the artificial seed bank experiments support conclusions from the afterripening laboratory experiments, which showed that afterripened cheatgrass germinates more rapidly than afterripened squirreltail. The germination of squirreltail populations may be too slow to facilitate fall emergence in some habitats. For example, mountain population seeds that fall-emerge face a higher risk of winter mortality; therefore, germination may be postponed to avoid death. These adaptive

mechanisms for cheatgrass and squirreltail permit fall emergence when it is advantageous for survival. However, our data suggest that early fall seeding of squirreltail into cheatgrass infested rangelands could be effective in future restoration projects. Further studies are needed to examine seedling establishment and competition between the two species.

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Table 1. Species and habitat information for seed collection sites.

Species	Location	Elevation (m)	Habitat Type
Cheatgrass	Whiterocks UT	1,450	Cold Desert
Cheatgrass	E. Green River UT	1,280	Salt Desert
Cheatgrass	E. Salina UT	2,040	Mountain Brush
Cheatgrass	N. Helper UT	2,070	Mountain Meadow
Squirreltail	Whiterocks UT	1,450	Cold Desert
Squirreltail	S. Price UT	1,340	Salt Desert
Squirreltail	E. Salina UT	2,040	Mountain Brush
Squirreltail	Strawberry UT	2,400	Mountain Meadow

Table 2. Location and habitat information for field sites used in artificial seed bank experiments with cheatgrass and squirreltail collections.

Location	Elevation (m)	Habitat Type	Annual Precipitation (cm)
Whiterocks	1,450	Cold Desert	18
Point of the Mountain	1,480	Mountain Brush	43
Strawberry	2,400	Mountain Meadow	65

Table 3. Mean germination percentage and mean germination time (days to 50% total germination) for recently harvested and fully afterripened seeds. Main effects and interactions are averaged across different treatments (i.e., species, habitat, incubation temperature). All main effects and interactions were highly significant ($p<0.0001$) for both response variables (AR=afterripening status).

	Recently Harvested Seeds		Fully Afterripened Seeds	
Effects & Interactions	Mean % Germ.	Mean Germ. Time	Mean % Germ.	Mean Germ. Rate
AR Main Effect (Avg. Species-Habitat-Incubation Temp.)	63%	13.4 days	100%	4.4 days
Cheatgrass (Avg. Habitat-Incubation Temp.)	50%	15.7 days	100%	3.0 days
Squirreltail "	77%	11.3 days	100%	5.9 days
Cold Desert Habitat (Avg. Species-Incubation Temp.)	44%	15.4 days	100%	4.2 days
Salt Desert Habitat "	52%	13.9 days	100%	4.1 days
Mountain Brush Habitat "	77%	11.3 days	99%	4.0 days
Mountain Meadow Habitat "	78%	13.2 days	100%	5.5 days
5/15°C Incubation (Avg. Species-Habitat.)	59%	13.2 days	99%	7.4 days
10/20°C Incubation "	83%	10.9 days	100%	4.1 days
15/25°C Incubation "	70%	12.8 days	100%	3.2 days
20/30°C Incubation "	40%	17.2 days	100%	3.1 days

Figure Legends

Figure 1. Germination percentages at four incubation temperatures for recently harvested and fully afterripened cheatgrass and squirreltail seeds from four habitats.

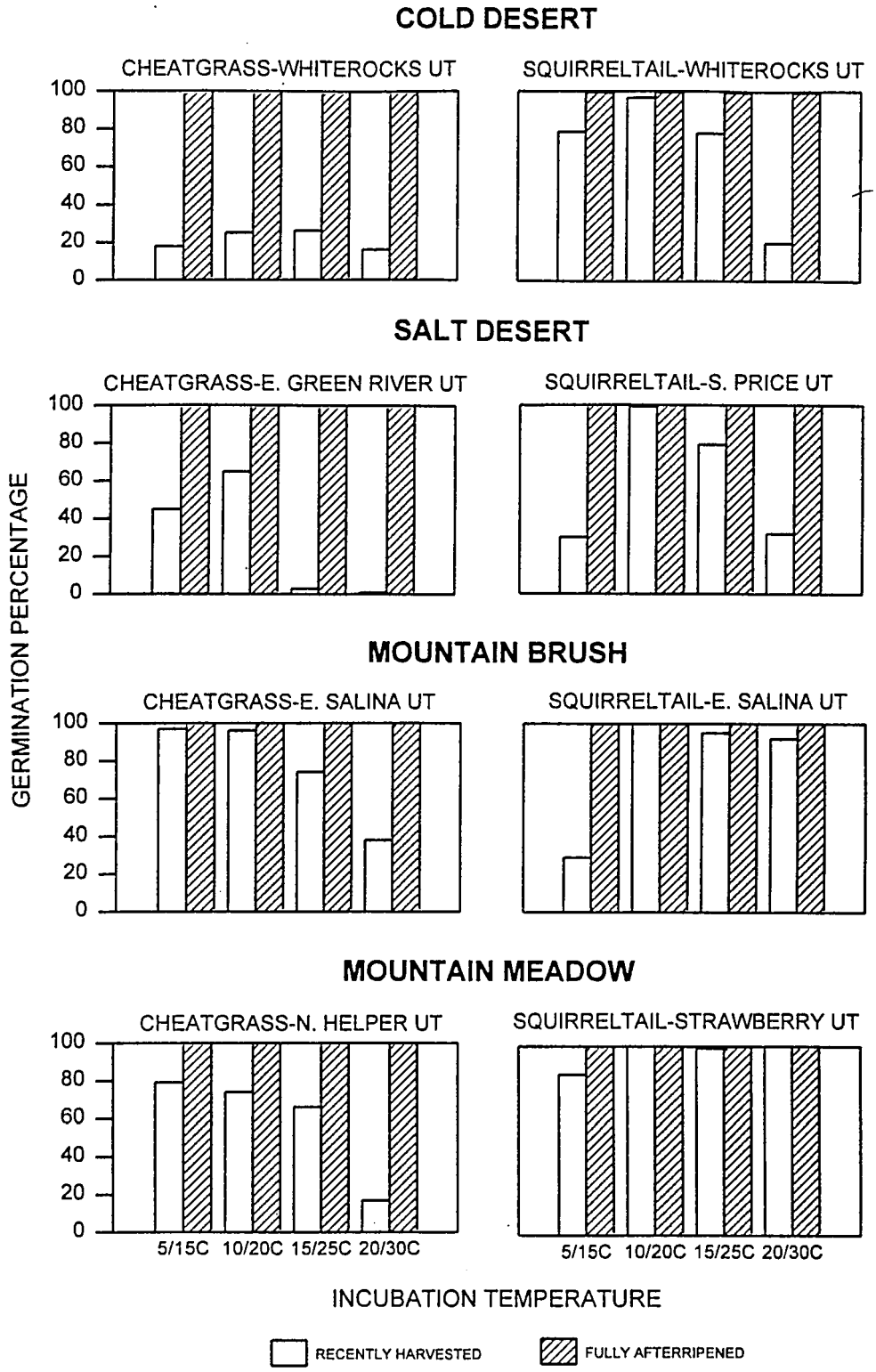
Figure 2. Mean germination time (days to 50% total germination) at four incubation temperatures for recently harvested and fully afterripened cheatgrass and squirreltail seeds from four habitats.

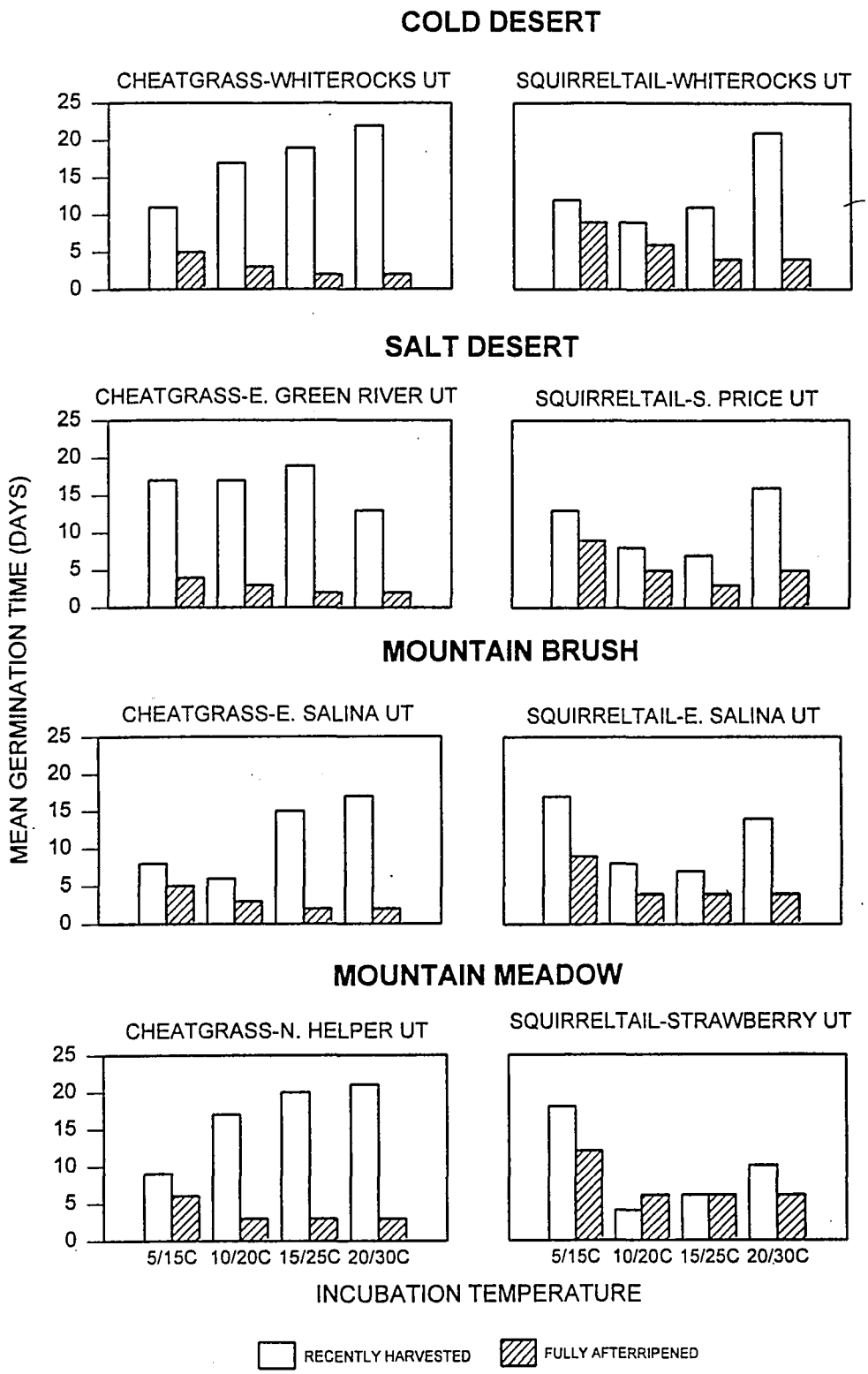
Figure 3. The effect of storage duration and temperature on mean germination time (days to 50% total germination) at four incubation temperatures for cold desert cheatgrass and squirreltail collections.

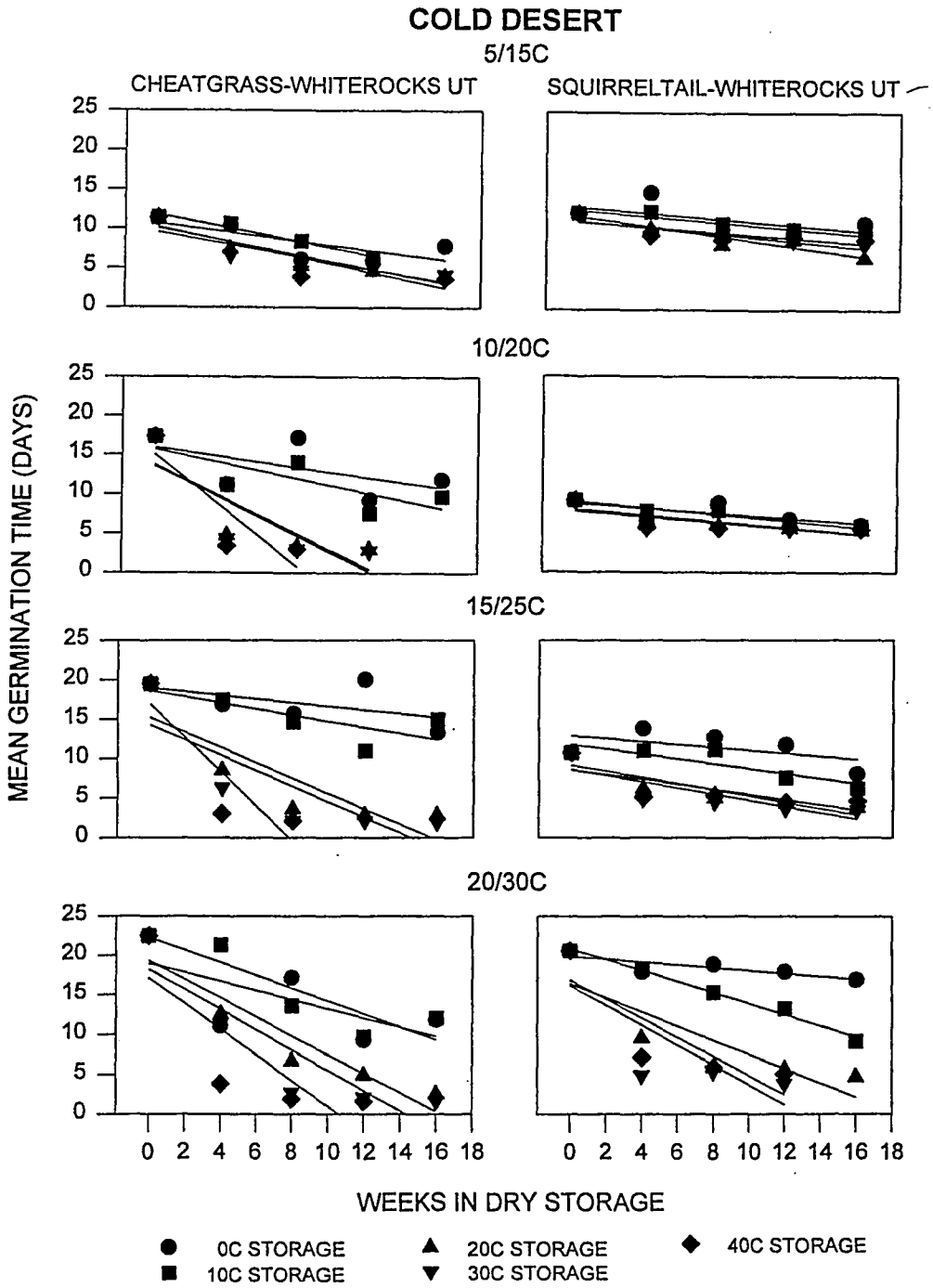
Figure 4. The effect of storage duration and temperature on mean germination time (days to 50% total germination) at four incubation temperatures for mountain meadow cheatgrass and squirreltail collections.

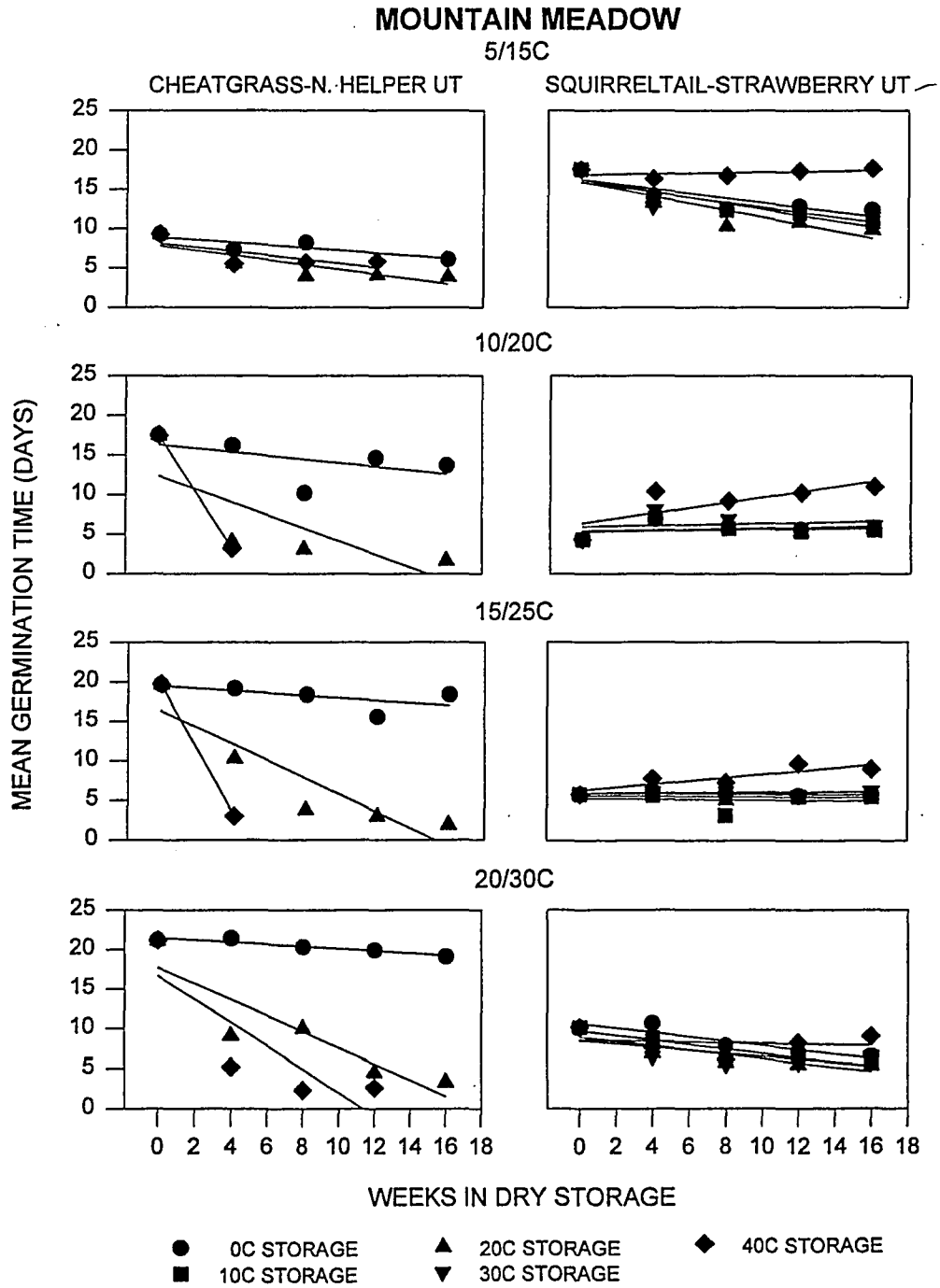
Figure 5. Field germination percentages for cheatgrass and squirreltail collections retrieved from artificial seed bank at Whiterocks, Point of the Mountain, and Strawberry field sites in late summer.

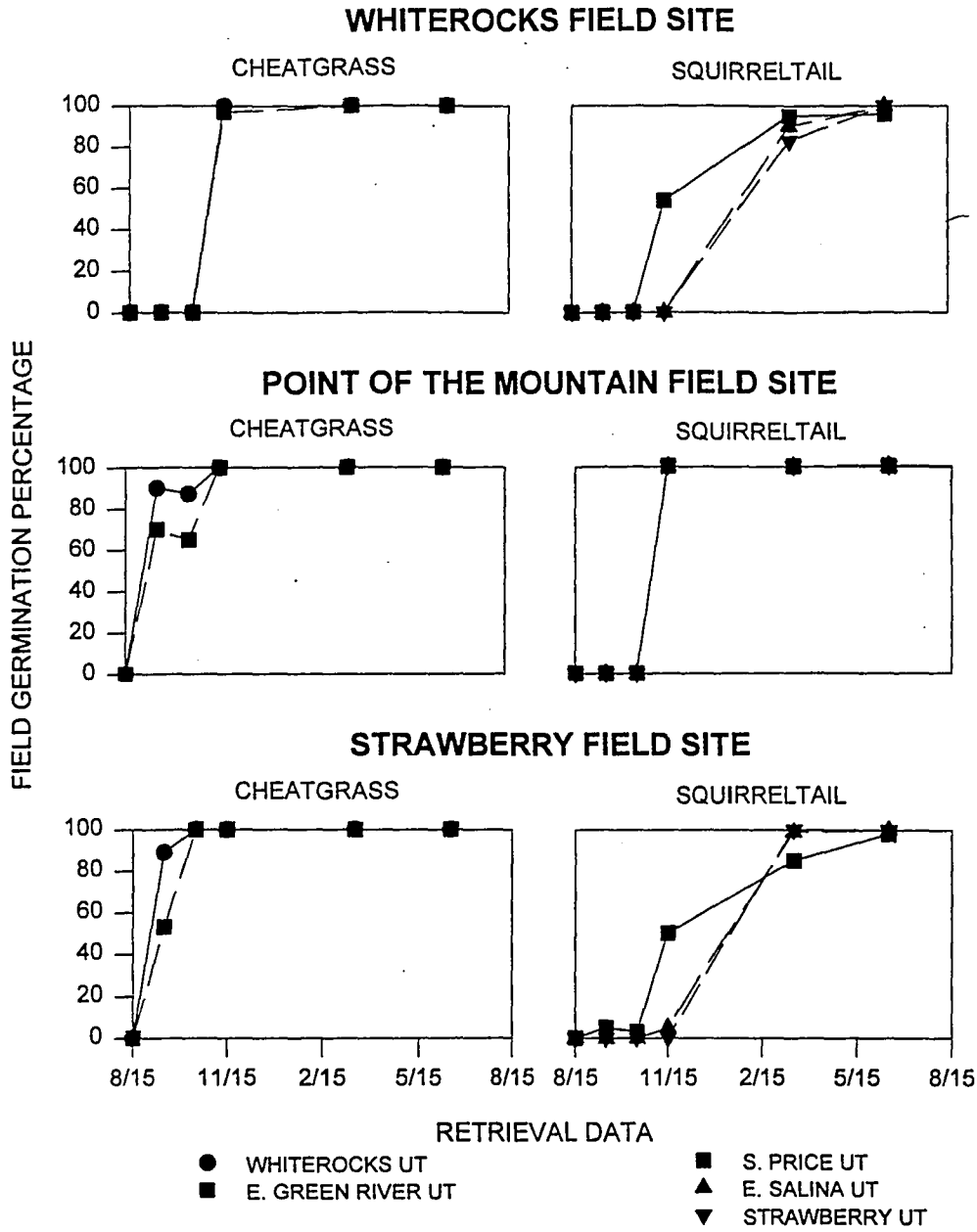
Figure 6. Climate diagrams for cheatgrass and squirreltail seed collection sites: cold desert, salt desert, mountain brush, and mountain meadow.

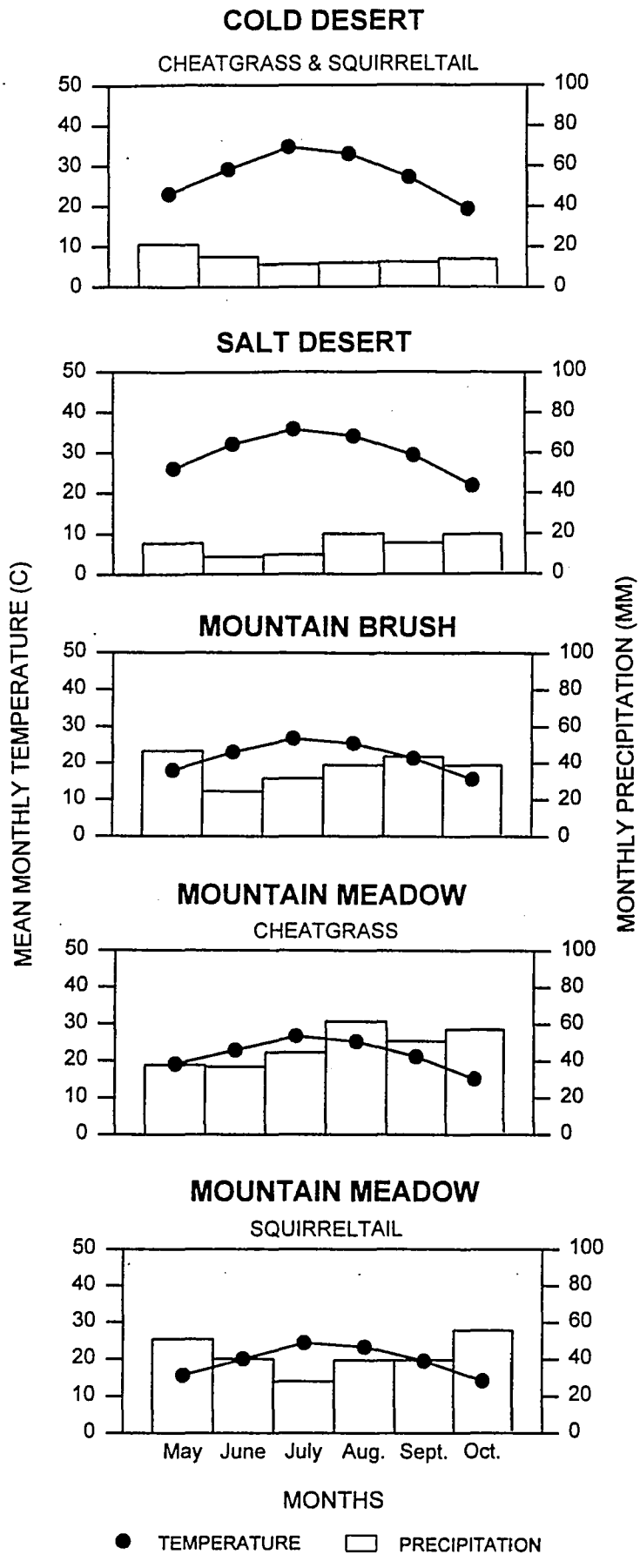

COLD DESERT
CHEATGRASS-WHITEROCKS UT
SQUIRRELTAIL-WHITEROCKS UT
SALT DESERT
CHEATGRASS-E. GREEN RIVER UT
SQUIRRELTAIL-S. PRICE UT
MOUNTAIN BRUSH
CHEATGRASS-E. SALINA UT
SQUIRRELTAIL-E. SALINA UT
MOUNTAIN MEADOW
CHEATGRASS-N. HELPER UT
SQUIRRELTAIL-STRAWBERRY UT
GERMINATION PERCENTAGE
100
80
60
40
20
0
5/15C 10/20C 15/25C 20/30C
INCUBATION TEMPERATURE
RECENTLY HARVESTED
FULLY AFTERRIPENED


COLD DESERT
CHEATGRASS-WHITEROCKS UT
SQUIRRELTAIL-WHITEROCKS UT
SALT DESERT
CHEATGRASS-E. GREEN RIVER UT
SQUIRRELTAIL-S. PRICE UT
MOUNTAIN BRUSH
CHEATGRASS-E. SALINA UT
SQUIRRELTAIL-E. SALINA UT
MOUNTAIN MEADOW
CHEATGRASS-N. HELPER UT
SQUIRRELTAIL-STRAWBERRY UT
MEAN GERMINATION TIME (DAYS)
25
20
15
10
5
0
5/15C 10/20C 15/25C 20/30C
INCUBATION TEMPERATURE
RECENTLY HARVESTED
FULLY AFTERRIPENED


COLD DESERT
5/15C
CHEATGRASS-WHITEROCKS UT
SQUIRRELTAIL-WHITEROCKS UT
10/20C
15/25C
20/30C
MEAN GERMINATION TIME (DAYS)
0 5 10 15 20 25
0 2 4 6 8 10 12 14 16 18
WEEKS IN DRY STORAGE
0C STORAGE
10C STORAGE
20C STORAGE
30C STORAGE
40C STORAGE


MOUNTAIN MEADOW
5/15C
CHEATGRASS-N. HELPER UT
SQUIRRELTAIL-STRAWBERRY UT
10/20C
15/25C
20/30C
MEAN GERMINATION TIME (DAYS)
0 5 10 15 20 25
0 2 4 6 8 10 12 14 16 18
WEEKS IN DRY STORAGE
0C STORAGE
10C STORAGE
20C STORAGE
30C STORAGE
40C STORAGE


WHITEROCKS FIELD SITE
CHEATGRASS
SQUIRRELTAIL
100
80
60
40
20
0
POINT OF THE MOUNTAIN FIELD SITE
CHEATGRASS
SQUIRRELTAIL
STRAWBERRY FIELD SITE
CHEATGRASS
SQUIRRELTAIL
FIELD GERMINATION PERCENTAGE
8/15
11/15
2/15
5/15
8/15
RETRIEVAL DATA
WHITEROCKS UT
E. GREEN RIVER UT
S. PRICE UT
E. SALINA UT
STRAWBERRY UT


COLD DESERT
CHEATGRASS & SQUIRRELTAIL
SALT DESERT
MOUNTAIN BRUSH
MOUNTAIN MEADOW
CHEATGRASS
MOUNTAIN MEADOW
SQUIRRELTAIL
MEAN MONTHLY TEMPERATURE (C)
MONTHLY PRECIPITATION (MM)
0
10
20
30
40
50
0
20
40
60
80
100
May June July Aug. Sept. Oct.
MONTHS
TEMPERATURE
PRECIPITATION

Germination Ecophysiology of Basin Wildrye (Leymus cinereus: Poaceae)[1]

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[1] This research was supported in part by funds provided by the Intermountain Research Station, Forest Service, U.S. Department of Agriculture.

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ABSTRACT

Basin wildrye is a common native perennial bunchgrass widely distributed in western North America. We studied seed germination responses of 41 collections from six states. Collections made in 1987 and 1988 were largely nondormant in mid-autumn but relatively slow to germinate at optimal temperatures (mean germination time 6 to 16 days). Seeds germinated more quickly after a 2-week chilling pretreatment (mean germination time 2 to 11 days). Mean germination time under conditions simulating prolonged snowpack (1C) varied among collections from 6 to 12 weeks and was negatively correlated with collection site mean January temperature, i.e., seeds from sites with colder, snowier winters germinated more slowly at near-freezing temperatures. In dry-afterripening experiments with four 1992 collections, basin wildrye seeds showed only minor change in germination rate and percentage after time in dry storage, unlike seeds of cheatgrass (Bromus tectorum) and squirreltail (Elymus elymoides), which are facultatively fall-emerging. Field retrieval studies showed that basin wildrye seeds did not germinate in autumn even under conditions that triggered complete germination of cheatgrass and squirreltail. Thus basin wildrye is primarily a spring-emerging species in spite of the fact that its seeds are mostly nondormant at dispersal. Its failure to germinate faster as a consequence of time in dry storage protects it from fall emergence under most weather scenarios. Timing of germination under snowpack is keyed to site-specific variation in snowpack duration, ensuring rapid emergence in very early spring. These results show the importance of rate as a mechanism that regulates germination phenology under semiarid conditions.

Basin wildrye (Leymus cinereus, Poaceae) is an important native bunchgrass widely distributed in western North America. It occurs over a broad range of habitats, including river valleys and swales in greasewood and basin big sagebrush communities, as well as in Wyoming big sagebrush, pinyon-juniper, mountain brush, and subalpine meadow types. It usually occupies slightly more mesic run-on microsites, especially at lower elevations. A cool-season grass, it flowers in early to midsummer. Lower elevation populations ripen seed in early July while seed of high montane populations may not be ripe until late September. As a bunchgrass, basin wildrye relies primarily on recruitment from seed for stand replacement and expansion.

Basin wildrye-dominated vegetation was formerly much more extensive than it is now. Abusive grazing and mowing practices as well as clearing for farmland and urban development have been largely responsible for this reduction (Young et al.1975). Restoration of riparian and subriparian areas in the Intermountain West will necessarily involve reestablishment of this species, primarily through direct seeding.

Interest in reestablishment of basin wildrye stands has led to the development of released cultivars, first "Magnar" (Howard 1979) and more recently "Trailhead". A major selection criterion has been good seed production, both in terms of yield and of quality (Evans and Young 1983). Seed quality has been considered a problem in collections from native stands (Young and Evans 1981).

A knowledge of germination ecophysiology and how it varies among populations should be helpful in efforts to develop seed sources of basin wildrye and to direct-seed it successfully. Young and Evans (1981) examined variation in germination

response to reduced osmotic potentials as a function of collection site edaphic characteristics. They found that collections from more saline-sodic soils were more conservative in their germination response under salt stress than those from nonsaline environments. They postulated that the saline soil populations were adapted to delay germination till early spring, when snowmelt would temporarily lower the salinity of the seed zone and after seeds had undergone some osmotic adjustment over the winter. Evans and Young (1983) also studied temperature responses of basin wildrye ("Magnar" and "P-05590"). They found the seeds to be highly germinable (viable and nondormant) at autumn-spring temperatures but to be delayed in germination at colder temperatures and largely inhibited at summer temperatures. Mean germination time (time to 50% of total germination) for "Magnar" (the faster accession) was almost a week even at optimum temperatures.

Studies to date have not dealt with the effects of dry storage or moist chilling on subsequent germination rate, percentage, and temperature sensitivity. Because basin wildrye seeds ripen in summer, they are likely to be exposed to a period of warm, dry conditions prior to any germination opportunity. And if they spring-emerge as postulated by Young and Evans (1981), their exposure to winter conditions could have a dramatic effect on their spring germination rate.

The studies presented here were designed to: 1) Determine the germination response of basin wildrye seeds to laboratory-simulated environmental cues, 2) Relate variation in basin wildrye germination response to habitat differences, 3) Develop a predictive model for basin wildrye field germination phenology based on laboratory

responses and test it in field retrieval experiments, and 4) Compare laboratory germination response and field germination phenology of basin wildrye to that of other summer-ripening grasses found in similar habitats.

The first part of our study (1987 and 1988 collections) examined the effects of short and long chilling periods on dormancy status and germination rate for seeds from basin wildrye populations across the whole spectrum of habitat types. We wanted to determine whether basin wildrye was likely to be facultatively fall-emerging or obligately spring-emerging. For a facultatively fall-emerging species, we hypothesized that rapid afterripening would lead to low dormancy and rapid germination at autumn temperatures, especially in populations from habitats with high probability of successful fall establishment (e.g., as in blue flax; Meyer and Kitchen 1994). For an obligately spring-emerging species, we hypothesized high dormancy and/or slow rate under autumn conditions, with little dry-afterripening or habitat-correlated variation (e.g., as in antelope bitterbrush; Meyer and Monsen 1989). Response to cues simulating winter chilling would be more likely to be habitat-correlated in obligately spring-emerging species than cues associated with autumn conditions (e.g., as in big sagebrush and rubber rabbitbrush; Meyer and Monsen 1992; Meyer et al. 1989).

The second part of our study (1992 collections) dealt explicitly with changes that take place during dry periods in summer and autumn. Species whose seeds show major changes in dry storage are those that ripen in summer, avoid risk of summer germination by being dormant or having slow rates, and yet must be ready to germinate quickly and completely in the fall. Experiments initiated in autumn with

seedlots collected at different times during summer might show differences between populations, but without evaluating changes during storage we could not be certain that these differences were not due simply to differences in seed age. Seed retrieval experiments were used to test the hypothesized relationships between laboratory germination patterns and germination phenology in the field.

MATERIALS AND METHODS

Seeds (caryopses with associated lemma and palea) collected in 1987 and 1988 were hand-stripped when fully ripe from stalks of at least twenty individuals at 34 locations (Table 1). Collections were cleaned in a small fanning mill and stored under laboratory conditions (ca. 20C, 7-8% moisture content) until experiments were initiated in mid-October each year. Seeds were handpicked for inclusion in experiments on a light table to ensure high fill. For each treatment, four replications of 25 seeds were used. Seeds were placed on the surface of two germination blotters (Anchor Paper, St. Paul MN) inside 100 X 10 mm plastic petri dishes kept saturated with tapwater. Treatments consisted of no chilling, 2-week chilling, and 20-week chilling. Chilling treatments were carried out in the dark in a 1C walk-in cold room, while 4-week post-chilling incubation was at 15/25C (12h:12h), a regime determined to be at or near optimum for this species (Evans and Young 1983; Allen et al. 1986). Germinated seeds (radicle >2mm) were counted and removed at least weekly during chilling and post-chilling incubation. In 1987, seeds were incubated in the dark and exposed to cool-white fluorescent light only during counts. In 1988, seeds were incubated with a 12-hour photoperiod, with high temperature coinciding with light. At the end of the 4-

week incubation period, viability of ungerminated seeds in each dish was determined using tetrazolium staining (Grabe 1970). Germination percentages were converted to a viable seed basis prior to analysis. Mean germination time (time to 50% of total germination) was interpolated from germination time course plots for each accession and treatment.

Mean January temperature at the collection site was obtained for each collection by interpolating on isotherm maps, supplemented with information from nearby weather stations when available (Water Information Center 1974; Stevens et al. 1983). This variable is used as a surrogate for an unavailable variable, mean duration of winter snow cover.

The relationships between mean germination time, chilling treatment (no chill versus 2-week chill), and collection site mean January temperature were examined for each collection year (1987 and 1988) using analysis of covariance (ANCOVA) procedures with mean January temperature as the covariate and chilling treatment as the class variable. Change in germination percentage in response to 2-week chilling was evaluated for each accession using a t-test.

Seedlots used in the 1992 storage experiments were collected from four Utah locations and cleaned as described above (Table 2). Within 2 weeks of harvest, seeds were placed under controlled storage conditions at 0, 20, and 40C. Recently-harvested seeds were hand-selected on a light table and placed in germination experiments using the protocols described above, except that viability at the end of incubation was determined by cut test (bisecting the seed and determining whether

embryo tissues are sound). Incubation (12-hour photoperiod) was carried out under the following 12h:12h temperature regimes: 5/15,10/20,15/25, and 20/30C. The experiment was repeated after 4, 8, 12, and 16 weeks of storage. A 10-week chilling treatment followed by incubation at 10/20C was included following 0 and 12 weeks of storage.

Germination percentage (viable seed basis) and mean germination time (days to 50% of total germination) were determined for each replication and subjected to analysis of variance (ANOVA) with accession, storage temperature, storage duration, and incubation temperature as the class variables. Linear regression was used to examine progressive changes in mean germination time as a function of storage duration for each accession-storage temperature-incubation temperature combination.

Field seed retrieval experiments were carried out with three of the four 1992 seed collections (Rush Valley was not included because of insufficient seed). Groups of approximately 100 seeds (determined by weight) were placed in flat nylon mesh packets. In mid-September, the packets were buried at a depth of 0.5 cm in groups that also included cheatgrass (Bromus tectorum) and squirreltail (Elymus elymoides) accessions. Each group of packets was protected with a hardwarecloth cone. The cones were arranged in three blocks at each of three field sites, a salt desert shrubland site (Whiterocks), a mountain brush site (Point of the Mountain) and a high elevation mountain meadow site (Strawberry; Table 3). In mid-October, mid-November, mid-March (mid-May at Strawberry) and mid-June, three sets of packets were retrieved from each site and transported to the laboratory in an insulated chest.

Within 6 hours following retrieval, germinated seeds in each packet were counted, and remaining seeds were placed in petri dishes, incubated at 10/20C for four weeks, and scored at least weekly for germination as described for laboratory experiments above. Seeds germinating during incubation were classed as ungerminated but laboratory-germinable, while any viable seeds remaining at the end of four weeks were classed as dormant.

RESULTS

Laboratory Experiments with 1987-1988 Seed Collections

Most 1987 and 1988 basin wildrye collections were nondormant at 15/25C when tested in mid-October following the summer of collection (Table 1). Mean germination percentage without chilling was 91% for the 1987 collections and 95% for the 1988 collections. Only six collections showed germination percentages of less than 85% without chilling. Germination percentage was significantly affected by two weeks of chilling for only two collections; both showed an increase relative to unchilled seeds.

Mean germination time for unchilled seeds at 15/25C varied among collections in both 1987 and 1988 (Figure 1). ANCOVA 's for these data showed that chilling caused a significant decrease (main effect, $p<0.0001$, for each year) in mean germination time. The decrease was greater for 1987 collections. Mean germination times for 1987 collections averaged 11.7 days without chilling and 3.9 days following two weeks of chilling. The average times for 1988 collections were 10.1 days without chilling and 6.6 days following two weeks of chilling. The negative relationship between mean germination time and collection site mean January temperature was

significant ($p<0.05$) only for 1987 collections. The slope of this relationship did not change significantly when seeds were chilled (mean January temperature x chilling treatment interaction, n.s., for each year). The fact that 1987 seeds were incubated in the dark while the 1988 seeds were incubated with a 12-hour photoperiod may explain the difference between years. It appears that the effects of collection site mean January temperature and short chilling on mean germination time were more pronounced when seeds were incubated in the dark.

When basin wildrye seeds were placed for 20 weeks under conditions simulating winter snow cover, most viable seeds germinated during chilling, and no dormant seeds remained after a week of post-chilling incubation at 10/20C. Mean germination time varied from 6 to 12 weeks and was significantly negatively correlated ($p<0.01$) with collection site mean January temperature for both years of collection (Figure 2). Collections from sites with long, cold, snowy winters took longer to germinate under snowpack-simulating conditions than collections from sites with short, mild, dry winters. ANCOVA showed that the slope and intercept of this relationship did not vary between years; the two regression lines do not differ statistically.

Laboratory Experiments with 1992 Seed Collections

Recently-harvested seeds of basin wildrye collected in 1992 were largely nondormant except at the lowest incubation temperature (5/15C), and this was the only incubation temperature that showed any significant effect of afterripening in dry storage on germination percentage (Table 4). Maximum germination percentages were significantly greater than recently harvested seed germination percentages for all

four collections at this incubation temperature. The Rush Valley collection was significantly more dormant overall than the other three collections, and this difference was most pronounced at the lowest incubation temperature.

Mean germination time did not decrease dramatically following dry storage. Of the four collections, only the Rush Valley collection showed any pattern of decreasing germination time with storage (Figure 3). For this collection, significant decreases in mean germination time at each incubation temperature took place during 16 weeks of storage at 20 and 40C, while changes during 0C storage were usually not significant (Table 5). Mean germination time at 5/15C changed from 20 days to 14 days, while the change at 10/20C was from 15 days to 8 days. The change at the optimum temperature of 15/25C was less, from 11 days to 8 days, while the change at the superoptimum temperature of 20/30C was from 14 days to 8 days. Even fully afterripened seed required at least a week to reach 50% germination, across the whole range of incubation temperatures.

Two of the remaining three collections, Pinto and Indian Canyon, were similar to each other in their responses in the dry storage experiment (Figure 3; Table 5). Both were midseason-ripening collections from middle elevations. Their mean germination times when freshly harvested were generally shorter at a given incubation temperature than the Rush Valley collection, but they changed less during storage, so that their mean germination times when fully afterripened were comparable.

The late-ripening high elevation Strawberry collection germinated slowly when recently harvested and showed no consistent tendency to accelerate its rate as a

consequence of time in dry storage (Figure 3; Table 5). The high variation associated with this collection and especially its reduced rates after prolonged storage at 40C may be related to its initial low viability (Table 2).

Germination percentages during 10 weeks at 1C showed contrasting patterns of change during storage for different accessions (Table 6). The high elevation Strawberry collection showed a low germination percentage when recently harvested, and this percentage did not rise significantly after 12 weeks at any of the three storage temperatures. The middle elevation Pinto and Indian Canyon collections both showed relatively high percentages when recently harvested but only minor increases after 12 weeks in storage. The Rush Valley collection was the only one to change substantially in its low temperature germination response during 12 weeks of dry storage. It started out with a low percentage when freshly harvested, and its percentage increased significantly during 12 weeks of dry storage as a direct function of storage temperature.

Field Retrieval Studies with 1992 Seed

At the salt desert shrubland Whiterocks site, there was no field germination of basin wildrye seeds during the two months of autumn after burial in mid-September 1992 (Figure 4). When packets were excavated from beneath the snow in mid-March 1993, germination percentages ranged from 29% for the Strawberry collection to 54 and 66% for the Pinto and Indian Canyon collections. By mid-June all viable seeds of all three collections had completed germination.

At the mountain brush Point of the Mountain site, there was no basin wildrye field

germination during the first month after burial. Slightly less than 10% of the viable seeds germinated from mid-October to mid-November, with no major between-collection differences. When packets were excavated from beneath the snow in mid-March, germination percentages ranged from 33 and 39% for the Pinto and Strawberry collections to 81% for the Indian Canyon collection. Again, all viable seeds had germinated by mid-June.

At the high elevation Strawberry site there was no autumn field germination of basin wildrye seeds. When seeds were excavated from under the snow in mid-May 1993, field germination percentages varied from 85 to 95% with no major between-collection differences. By mid-June all viable seeds had germinated.

All viable ungerminated basin wildrye seeds retrieved from the field germinated readily in laboratory incubation, and there was no evidence for any secondary dormancy or provision for between-year carryover of ungerminated seeds. All viable seeds had germinated in the field by the end of the first spring after dispersal regardless of the xericness of the site, and the majority of these seeds actually germinated under snowpack during the winter.

Very few if any basin wildrye seeds germinated in autumn prior to the onset of chilling; the few seeds that germinated in November at Point of the Mountain apparently did so during a thaw that followed an early snowstorm. At the higher elevation Strawberry location this storm initiated the period of continuous winter snowpack; the mid-November retrieval was from beneath snow. Failure to germinate prior to chilling was not due to lack of autumn precipitation. Cheatgrass and

squirreltail seedlots placed beneath the same cages had germinated fully by mid-October at Point of the Mountain and by mid-November at the other two sites (Beckstead et al. in press).

DISCUSSION

The field germination phenology of basin wildrye seeds is regulated through germination rate rather than through dormancy. Most seeds are nondormant at dispersal in middle to late summer but are relatively slow to germinate across a wide range of temperatures. Germination is somewhat accelerated following dry storage, especially for earlier-ripening populations. But maximum rates are still too slow to permit substantial germination in response to autumn rains. Chilling under snow cover accelerates post-chilling germination, so that germination in spring is much more rapid than experiments with unchilled seeds would suggest. If snow cover persists for long enough (>6 to 12 weeks), substantial germination will take place beneath the snow, and rapid emergence will follow soon after snowmelt. There are no apparent mechanisms for the induction of secondary dormancy in the field, and there is little or no seed carryover across years even at more xeric sites.

We found some evidence for habitat correlated between-population variation in the germination responses of basin wildrye, particularly in terms of response to chilling. Mean germination time under continuous chilling was significantly less for collections from habitats where winter snow cover duration is shorter. This could function to ensure emergence at the earliest opportunity in spring in these habitats. Populations of more mesic, high elevation habitats had seeds that would delay germination until

later in winter. Between-population variation in the responses of unchilled seeds was only weakly habitat-correlated, as would be expected in a species whose seeds germinate in the field in response to chilling.

We did see some between-population variation in dry-afterripening patterns, although its ecological significance was unclear. The earliest-ripening Rush Valley seeds changed the most, while the late-ripening Strawberry seeds changed the least. Dry-afterripening in the Rush Valley seeds resulted in an increased low temperature germination rate, perhaps the most ecologically relevant change. When recently-harvested seeds were tested, Rush Valley seeds were as slow to germinate in chilling as high-elevation Strawberry seeds, with Pinto and Indian Canyon seeds germinating faster. But afterripened Rush Valley seeds showed the more rapid low temperature germination rate characteristic of sites with minimal winter snow cover. The habitat-correlated differences in low temperature mean germination time seen in 1987 and 1988 collections tested in mid-autumn may thus be at least partly a consequence of differences in dry-afterripening patterns that function to provide seeds with an appropriate low temperature response at the time they need it, i.e., when chilling commences in late autumn.

Dry-afterripening is known to be an important aspect of germination regulation for many grass species (Simpson 1990; Murdoch and Ellis 1992; Probert 1992). Most studies deal with loss of primary dormancy in dry storage and how rate of dormancy loss is related to storage conditions such as temperature. Very few afterripening studies (e.g., Ellis et al. 1987) report changes in mean germination time. Slow rate is

not an effective deterrent to germination in the mesophytic species most often studied. But in semiarid environments, where periods of adequate soil moisture are limited, slow germination rate can be functionally equivalent to dormancy.

Investigation of the causes of germination acceleration may provide clues as to why some grass species of the semiarid Great Basin are facultatively fall-emerging and others are not (Allen et al. 1994). Young and Evans (1977) state that neither cheatgrass nor squirreltail afterripen in dry storage; this may be true in terms of primary dormancy, at least for some collections. But we have found that major changes in germination rate take place as a consequence of time in dry storage for both these species (Beckstead et al. in press). The net result of these changes is that their seeds are protected from germination in early to midsummer when they are dispersed but are able to respond to autumn rains with rapid and often complete germination. Basin wildrye seeds do not undergo these dramatic changes in rate, and they fail to emerge in autumn as a consequence.

Germination under winter conditions is mediated through low temperature germination rate for many species of the semiarid Great Basin (e.g., big sagebrush, Meyer and Monsen 1992; rubber rabbitbrush, Meyer et al. 1989; penstemon species, Meyer 1992, Meyer and Kitchen in review). In a climate where winter precipitation is more reliable than precipitation during the growing season, chances for establishment are enhanced by emergence in very early spring, and conditions under snow cover provide seeds with a consistently moist, predictable environment for radicle growth.

In comparison to winter germination, germination in autumn in the Great Basin

environment is high risk at best. For a long-lived species such as basin wildrye, there may be no reproductive advantage to autumn establishment, whereas for an annual like cheatgrass, individuals that successfully autumn-establish may have greatly increased seed production relative to spring-emerging individuals (Mack and Pyke 1983). Also, because basin wildrye often grows in run-on microsites, its seedlings may experience more prolonged periods of spring moisture than seedlings of upland species.

ACKNOWLEDGMENTS

This research was supported in part by USDA Cooperative State Research Service Grant No. 87-CRSR-2-3154. We thank Stanley Kitchen and Stephanie Carlson for help with seed collection and Scott Walker for able technical assistance. Thanks also to the Lake Valley Turf Farm for permission to use the Point of the Mountain retrieval site.

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Table 1. Location and habitat, mean viability percentages, and mean germination percentages (expressed as percentage of viable seeds) at 15/25C with and without a 2-week chill for 20 1987 collections and 17 1988 collections of basin wildrye.[a]

Location	Elevation (m)	Plant Community	Mean Temp. January (C)	Viability %	Germination %	
					No Chill	2-wk Chill
1987 Collections						
Pinto UT	2,150	Pinyon-juniper	-1.1	84	100a	100a
Summer Lake OR	1,290	Greasewood	-2.2	71	97a	99a
N Yakima WA	430	Palouse prairie	-2.2	70	99a	100a
Jiggs Road NV	1,660	Wyoming big sagebrush	-3.3	69	75b	98a
Lamoille Canyon NV	2,090	Mountain brush	-3.9	96	74a	82a
Sheldon Refuge NV	1,660	Sagebrush-grassland	-3.9	88	85a	98a
S Wells NV	1,620	Wyoming big sagebrush	-3.9	81	96a	97a

Table 1.--continued.

Location	Elevation (m)	Plant Community	Mean Temp. January (C)	Viability %	Germination %	
					No Chill	2-wk Chill
S Baker OR	1,230	Sagebrush-grassland	-3.9	70	97a	94a
N Wells NV	1,820	Wyoming big sagebrush	-5.6	94	90a	100a
N Lapine OR	1,350	Ponderosa pine parkland	-5.6	90	73b	91a
Panguitch Lake UT	2,580	Ponderosa pine parkland	-6.1	93	97a	100a
N Sheridan WY	1,140	Shortgrass prairie	-6.7	82	86a	97a
Park City UT	2,090	Mountain brush	-6.7	83	91a	98a
Echo Canyon UT	1,970	Mountain brush	-7.8	91	88a	89a
Wahsatch UT	2,150	Mountain brush	-7.8	87	85a	87a
Kemmerer Jct. WY	2,120	Mountain brush	-8.3	90	85a	78a

Table 1.--continued.

Location	Elevation (m)	Plant Community	Mean Temp. January (C)	Viability %	Germination %	
					No Chill	2-wk Chill
Wamsutter WY	2,100	Wyoming big sagebrush	-8.3	78	87a	94a
Indian Canyon UT	1,850	Greasewood	-8.9	91	99a	100a
Strawberry UT	2,400	Mountain meadow	-8.9	61	59a	70a
1988 Collections						
Birds of Prey ID	920	Wyoming big sagebrush	-1.7	86	99a	98a
Montgomery Pass NV	2,090	Pinyon-juniper	-2.2	87	93a	89a
Bruneau ID	950	Wyoming big sagebrush	-2.8	86	100a	100a
Eagle ID	800	Sagebrush-grassland	-2.8	86	94a	86a
Jiggs Road NV	1,660	Wyoming big sagebrush	-3.3	90	99a	99a

Table 1.--continued.

Location	Elevation (m)	Plant Community	Mean Temp. January (C)	Viability %	Germination %	
					No Chill	2-wk Chill
Lamoille Cyn. NV	2,090	Mountain brush	-3.9	83	92a	81a
Lava Hot Springs ID	1,460	Sagebrush-grassland	-5.0	90	94a	89a
Fellini Rocks UT	2,090	Mountain brush	-5.0	88	100a	100a
Beacon Pit Mine NV	1,720	Wyoming big sagebrush	-5.6	81	88a	90a
Switzer Summit ID	1,600	Sagebrush-grassland	-5.6	87	98a	95a
Stone ID	1,380	Sagebrush-grassland	-5.6	71	100a	91a
Mink Creek ID	1,940	Mountain forest	-6.7	88	94a	89a
W Malad ID	1,690	Sagebrush-grassland	-7.2	80	88a	75a
Hailstone Jct. UT	1,900	Mountain brush	-7.8	83	97a	94a

Table 1.--continued.

Location	Elevation (m)	Plant Community	Mean Temp. January (C)	Viability %	Germination %	
					No Chill	2-wk Chill
Soldier Summit UT	2,280	Mountain meadow	-8.9	66	84a	86a
Strawberry UT	2,400	Mountain meadow	-8.9	77	88a	81a

[a]Within an accession (row) germination percentage means followed by the same lowercase letter are not significantly different at the $p<0.05$ level according to a Student's t-test.

Table 2. Location, habitat and viability information for 1992 basin wildrye collections.

Location	Elevation	Plant Community	Mean January Temperature (C)	Mean Viability Percentage
Rush Valley UT	1,660	sagebrush-grassland	-6.1	82
Pinto UT	2,150	pinyon-juniper	-1.1	86
Indian Canyon UT	1,850	pinyon-juniper	-8.9	84
Strawberry UT	2,400	mountain meadow	-8.9	60

Table 3. Location and habitat information for three field sites used in seed retrieval experiments with 1992 basin wildrye collections.

Location	Elevation	Plant Community	Mean January Temperature (C)	Annual Precipitation (cm)
Whiterocks	1,450	shadscale	-6.1	18
Point of the Mountain	1,480	sagebrush-grassland	-3.3	43
Strawberry	2,400	mountain meadow	-8.9	65

Table 4. Twenty-eight day mean germination percentages at four incubation temperatures for recently-harvested and maximally afterripened seeds of four 1992 basin wildrye collections (RH=recently harvested; AR=maximally afterripened; P=probability that values for RH and AR are significantly different).

Collection	Incubation Temperature											
	5/15C			10/20C			15/25C			20/30C		
	RH	AR	P	RH	AR	P	RH	AR	P	RH	AR	P
Rush Valley	32	61	.01	91	96	ns	86	99	ns	74	91	ns
Pinto	79	98	.01	100	100	ns	100	100	ns	98	100	ns
Indian Canyon	69	88	.01	100	100	ns	100	100	ns	95	100	ns
Strawberry	53	84	.01	96	100	ns	99	100	ns	98	98	ns

Table 5. Slopes and significance levels for linear regressions of mean germination times at four incubation temperatures on duration of storage at 0, 20, and 40C for four 1992 basin wildrye collections.[a]

Collection	Incubation temperature			
	5/15C	10/20C	15/25C	20/30C
Rush Valley				
0C Storage	n.s.	-0.208***	n.s.	n.s.
20C Storage	-0.313*	-0.247**	-0.233***	-0.236*
40C Storage	-0.286*	-0.415***	-0.240***	-0.457***
Pinto				
0C Storage	-0.152*	-0.099**	n.s.	+0.107*
20C Storage	n.s.	-0.151**	-0.058**	n.s.
40C Storage	n.s.	-0.167***	n.s.	n.s.
Indian Canyon				
0C Storage	-0.268***	-0.127**	n.s.	n.s.
20C Storage	-0.332***	-0.219***	-0.103***	-0.108**
40C Storage	n.s.	-0.129***	n.s.	-0.123*

Table 5.--continued.

Collection	Incubation temperature			
	5/15C	10/20C	15/25C	20/30C
Strawberry				
0C Storage	n.s.	-0.132*	n.s.	n.s.
20C Storage	n.s.	n.s.	n.s.	n.s.
40C Storage	+0.323**	-0.132**	n.s.	n.s.

[a]Significance levels denoted are: n.s.= not significant at $p<0.05$; * = significant at $p<0.05$; ** =significant at $p<0.01$; *** =significant at $p<0.001$.

Table 6. Mean germination percentages during 10 weeks at 1C for seeds of four 1992 basin wildrye collections tested when recently harvested and after 12 weeks of storage at 0, 20, and 40C. [a]

Collection	Storage Treatment			
	Recently Harvested	12 weeks-0C	12 weeks-20C	12 weeks-40C
Rush Valley	11c	23bc	35b	76a
Pinto	46b	43b	63a	56ab
Indian Canyon	45b	47b	63a	62a
Strawberry	14a	5a	18a	9a

[a] Within a collection (row), means followed by the same lowercase letter are not significantly different at the $p<0.05$ level according to the Student-Newman-Keuls means separation criterion.

Figure legends.

Figure 1. The relationship between collection site mean January temperature and mean germination time (days) at 15/25C for 1987 and 1988 basin wildrye collections incubated with or without a 2-week chilling pretreatment.

Figure 2. The relationship between collection site mean January temperature and mean germination time (weeks) for 1987 and 1988 basin wildrye collections incubated continuously at 1C for 20 weeks.

Figure 3. The effect of time in storage at 0, 20, and 40C on mean germination time (days) at four incubation temperatures for 1992 basin wildrye collections from Rush Valley, Pinto, Indian Canyon, and Strawberry.

Figure 4. Time course plots of field germination percentages for 1992 basin wildrye collections from Pinto, Indian Canyon, and Strawberry placed in seed retrieval experiments at the Whiterocks, Point of the Mountain, and Strawberry study sites in mid-September 1992. Each point represents the mean of three replications.

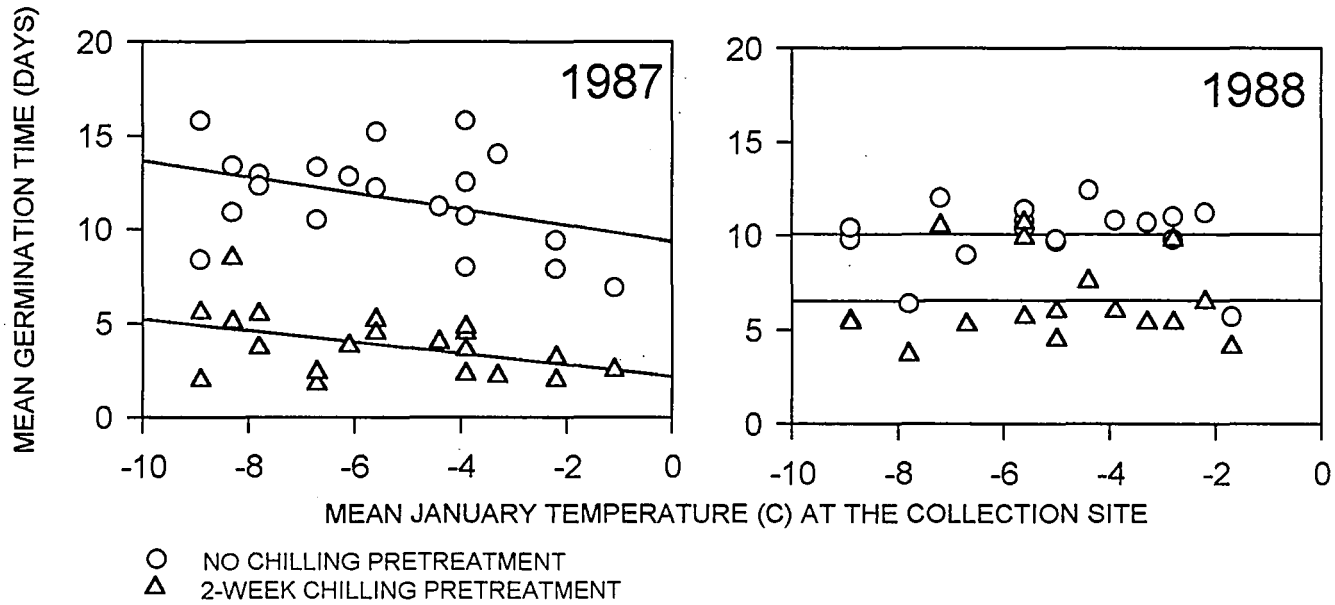
MEAN GERMINATION TIME (DAYS)
20
15
10
5
0
1987
1988
-10
-8
-6
-4
-2
0
MEAN JANUARY TEMPERATURE (C) AT THE COLLECTION SITE
NO CHILLING PRETREATMENT
2-WEEK CHILLING PRETREATMENT

Figure 1.

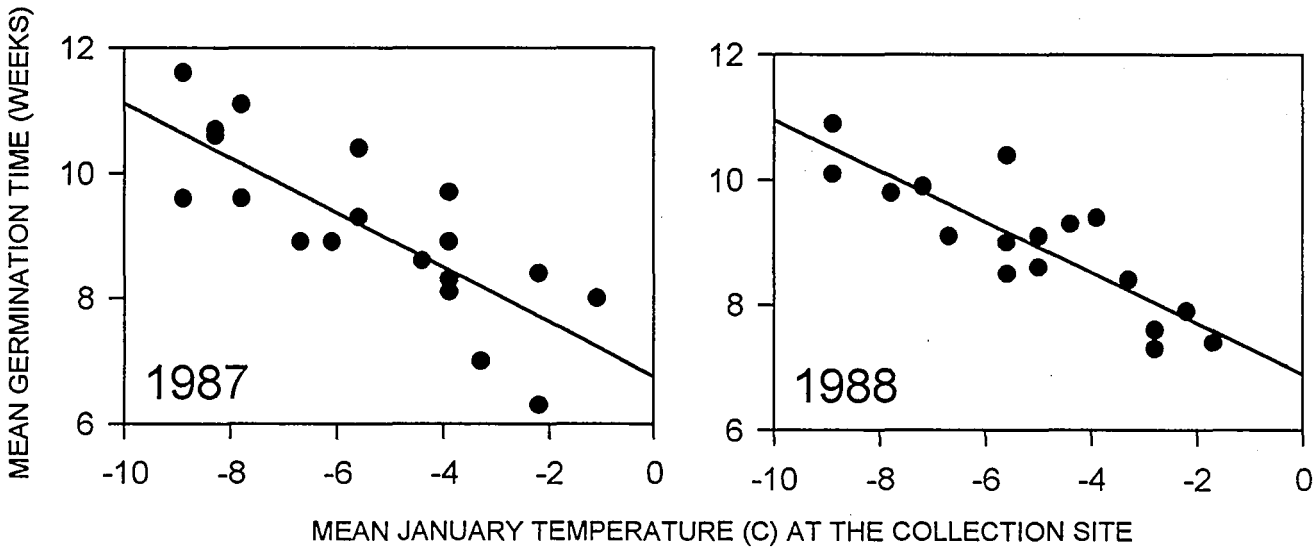
MEAN GERMINATION TIME (WEEKS)
12
10
8
6
1987
1988
-10
-8
-6
-4
-2
0
MEAN JANUARY TEMPERATURE (C) AT THE COLLECTION SITE

Figure 2.

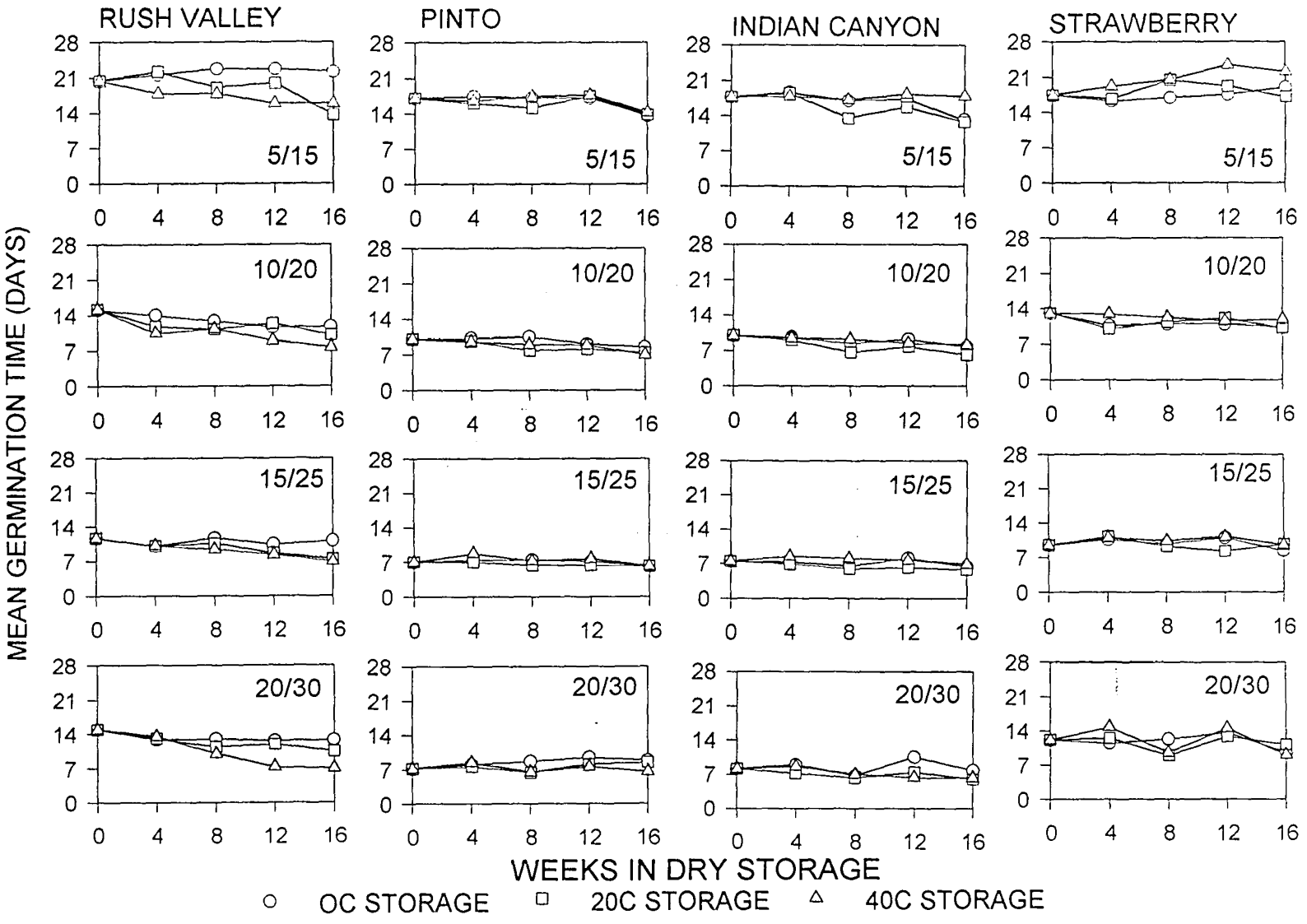
RUSH VALLEY
PINTO
INDIAN CANYON
STRAWBERRY
5/15
10/20
15/25
20/30
MEAN GERMINATION TIME (DAYS)
WEEKS IN DRY STORAGE
OC STORAGE
20C STORAGE
40C STORAGE

Figure 3.

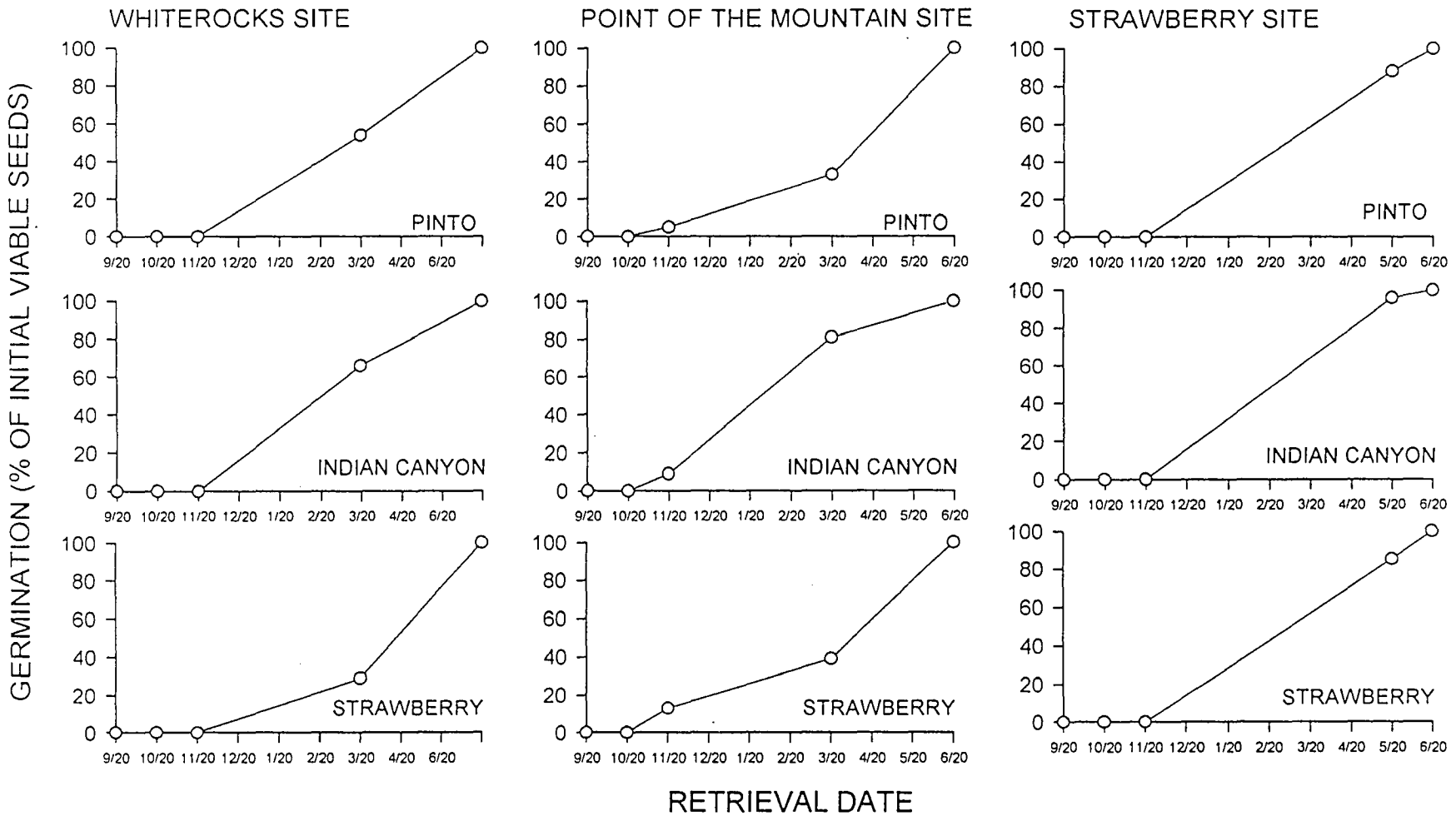
WHITEROCKS SITE
POINT OF THE MOUNTAIN SITE
STRAWBERRY SITE
GERMINATION (% OF INITIAL VIABLE SEEDS)
PINTO
INDIAN CANYON
STRAWBERRY
0
20
40
60
80
100
9/20 10/20 11/20 12/20 1/20 2/20 3/20 4/20 5/20 6/20
RETRIEVAL DATE

Figure 4.